THE ECOLOGICAL SIGNIFICANCE OF EMBANKMENT AND DRAINAGE WITH RESPECT TO THE VEGETATION OF THE SOUTH-WEST NETHERLANDS

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INTRODUCTION

About 6000 years ago the turbulent history of what is now the south-west part of the Netherlands began. At that time this region was a lagoon-like area isolated from the sea by sand barriers. These dune ridges were locally intersected by the river mouths of the Rhine, Meuse and Scheldt. After that time, during periods of increased marine ingression into the coastal barriers, invasion by the sea shifted the transition zone between salt and fresh water far inland. During these periods mainly marine sediments were deposited, and in the intervening regression periods peat formation took place. From Roman times until about 1000 A.D. the area was eroded from several inlets as a consequence of a renewed activity of the sea. Along deep erosion channels deposition of sand and silt took place, while mainly clay was deposited on the remaining peat islands. In this way a most complicated estuarine area was formed with the sea intruding from the west, and the rivers flowing in from the east, both exerting their influence upon the water–land boundary-system.

Subsequently man began to play an active role reclaiming the land remnants by means of throwing up mounds and dikes. Traditionally, the salt marshes were mostly occupied in the summer months only. Their inhabitants had to retire to higher ground for the winter. They were mainly stock farmers rearing sheep, some pigs, and cattle. Others were fishermen or were engaged in coastal trade. In the Carolingian and subsequent periods they threw up settlement mounds, just big enough to serve as the foundation for a single farmstead, as a refuge for livestock during times of flood, or solely to protect fresh water-holes from pollution by unusually high tides (cf. van Zeist 1968–70 and the excellent study by Lambert 1971). Although probably already in the seventh century some low sea-walls had been thrown up (van Rummelen 1965), in the eleventh and twelfth centuries the construction of dams was more practised as a means of defence against the tides. These first systematic embankments were started in the south (Flanders; see Gottschalk 1955) as well as in the north (near Vlaardingen by Frisian colonists; see Niermeyer 1958) mainly in those areas adjacent to the more or less protected higher ground (closed dune ridges and Pleistocene deposits). Probably starting from these parts of the periphery, embankment was practised all over the south-west part of the country (Fig. 1). Nowadays more than ten thousand kilometres of dikes enclose about a thousand polders in this region, forming a network of elevated sites in the otherwise nearly flat landscape.

Initially, the damming activities were solely to protect existing land remnants, not to reclaim new land. The building of dikes and the damming of creeks in these land remnants,

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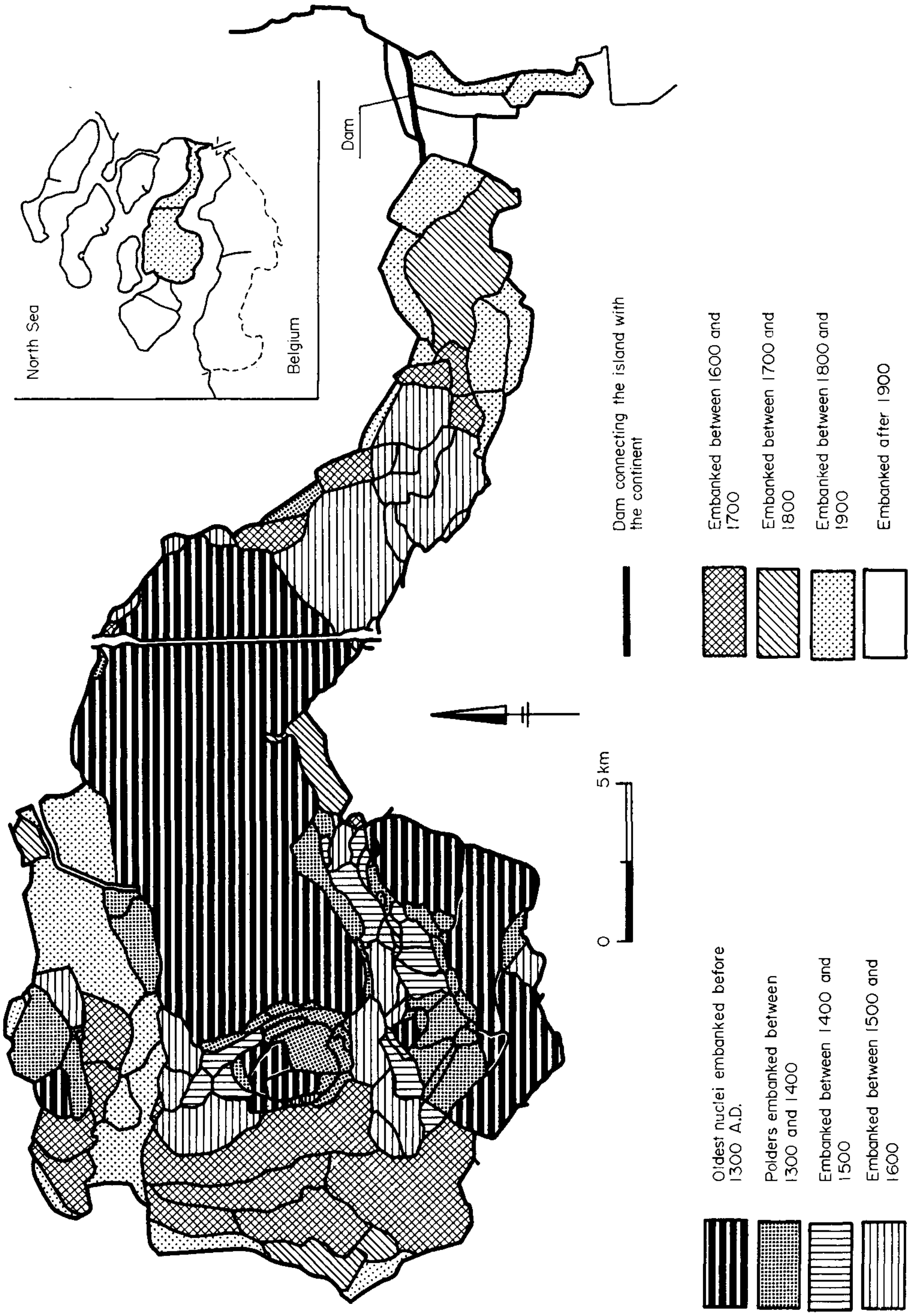


FIG. 1. History of embanking. The island of Zuid-Beveland.

however, protected vast parts of the higher marshes against flooding, and therefore prevented deposition of silt and sand. These conditions, together with the alternate transgression and retreat of the sea, promoted accretion and maturation as well as erosion processes in the remaining tidal marshes, and were the reason that the inhabitants could change from more conservative to more progressive methods of embankment. Obviously, other factors played an important role in the rate and policy of medieval embanking, especially demographic ones, such as the interest of monastic orders in land reclamation and the increasing density of the population (Gottschalk 1955). Salt marshes once used only for sheep and cattle grazing had transformed into polder areas suitable for tillage.

At the close of the Middle Ages many dike-bursts and flood disasters inflicted serious losses upon the area owing to (1) age-long digging and mining activities in the underlying peat formations for the purposes of salt-making and heating, (2) serious neglect of the maintenance of the dikes as a consequence of political troubles and religious quarrels, (3) inundation of polders as a result of cutting of dikes for military purposes, and (4) rise in sea-level, especially that of storm floods, caused partly by ingression of the sea, but particularly as a consequence of the narrowing of the sea-arms and estuarine branches by embankment, thus driving up the flood-waves to ever higher levels. According to Lambert (1971) the fifteenth century was a period in which the extension of cultivation made little progress, and, in some parts, even the opposite took place. For the time being the progress of the technology of impoldering failed to keep pace with the rise in sea-level. Since the invention of the simple one-way sluice valve in the tenth century there had been little further development in drainage techniques. The excess of polder water could be evacuated only by means of gravity flow, or the use of human or animal power operating simple scoops and water wheels. The wind-driven water mill was not brought widely into use until the seventeenth century (Lambert 1971). Meanwhile the continuing rise in the water-table, on account of the rise in sea-level and of the lowering of the land surface by shrinkage and digging of the peat, had turned over areas initially devoted to tillage to waterlogged pastures or hay lands.

In this way, man, creating his own environment, also changed the environment for plant and animal life. Together with the borders of ditches, ponds, watercourses and the old hummocky grasslands, the dikes form the most important habitats for plant life in the polderland, similar to the situation in the poldered areas of the British Fenland (Darby 1940, 1956; Tansley 1949). The present paper describes some aspects of the impact of embanking on the distribution of plants, especially on that of halophytes. In doing so, the concept of halophyte is taken in a wide sense, including species living in temporarily brackish environments. Plant nomenclature is according to the *Flora van Nederland* (Heukels & van Oostroom 1970).

The associations, alliances, etc. are floristically defined and named in accordance with the Braun-Blanquet system of the hierarchical classification of syntaxa (see Braun-Blanquet 1964; Shimwell 1971). The nomenclature of the syntaxa is that of the survey of Plant Communities in the Netherlands by Westhoff & den Held (1969).

THE NATURE OF MAN'S RECLAMATION ACTIVITIES IN TIDAL MARSHES

When the tidal water–land boundary is regarded as an ecosystem the influence of man must be considered as one of the important factors, in a similar sense as climate, tidal influences and soil conditions. However, human influence results in sharp lines of demarcation with sea-walls and ditches, barrages and canals. In the interest of man's own physical existence, his interference with the landscape is apt to promote a monotonous vegetation for animal husbandry and agriculture. Ancient embanking activities and mining systems, however, introduced several new types of environment, so increasing the spatial diversity in living conditions for plants and animals. Both levelling and differentiation of variety-in-space, owing to or in spite of man's intentions, may be considered as ecological side-effects of his reclamation activities. As van Leeuwen (1965) pointed out for the ecological impact of old-fashioned agricultural and mining systems dan Westhoff (1966) confirmed for that of traffic, also in the case of embanking, spatial diversity is favoured by (1) the small scale and gradual character of the operations, and (2) the persistence of traditional methods and the use of time-honoured materials until recent times. Modern coastal engineering, however, promotes increasing application of new technical methods, bridging distances through scale enlargement, and therefore breaking down spatial diversity, including that which has been built by man himself in former ages.

From studies dealing with the earliest reclamation measurements it is clear that man derived his first constructions directly from geomorphological components and tidal processes characteristic of the water–land boundary system itself. From the ecological point of view these environmental elements of 'pattern and process' may be called 'selectors', for they determine the degree of internal selectivity of the ecosystem (van Leeuwen 1967). All selectors combined constitute the system of non-living selection mechanisms within the ecosystem. This system forms the 'primitive' basis or 'matrix' for the much more complicated genetic mechanisms inherent in living nature. The latter do not only conform to the system of environmental selection mechanisms, but also refine and stabilize it, and thus other, more specialized, genetic mechanisms (species) will be added gradually through increase of niches.

In comparison with these environmental mechanisms even the medieval small-scaled regulation management of man leads to rather serious interference. Preferentially the environmental selectors inherent in the boundary system were used and modified for human purposes (Table 1). On natural elevations man threw up dwelling mounds (terps), refuges for himself and his cattle (Bennema & van der Meer 1952; Hageman 1964; van der Heide 1959; Vlam 1943; Lambert 1971), and, in low-salinity and freshwater tidal regions, hills were used for stacking reed and brushwood stocks. Creek- and river-banks, and sometimes beach-banks and dune-ridges, were reinforced and changed into sea-walls for the control of floods (de Bakker 1950; Bennema & van der Meer 1952; Vlam 1943). Creeks were closed at places where the tide-runs had formed a threshold (van Rummelen 1965).

At the same time, natural watercourses induced the idea of cutting field-drains, ditches, and fairways. Natural basins were considered as potential containers for drinking water, as places to arrange harbours and docks for navigation purposes, and as flood storage basins to catch water for flushing navigable tide-channels during low tide to keep them clear of mud. Moreover, man learned to combine his regulating mechanisms, for instance by fitting culverts in the dikes and under the roads, by erecting weirs with an overflow section in the creeks, and by constructing slipways for hauling vessels across a dam. The latter construction is described by Gottschalk (1955, p. 42) for Flanders and may form the precursor of the tide-lock or pound-lock. The periodic alternation of ebb and flood finally leads to the development of outlets with a one-way sluice valve, of tide-gates, tide-locks and of docks, in combination with embanking constructions.

All these early human operations must be considered as strongly interconnected, as each of them can be effective only when others are carried out as well. For instance,

Table 1. *Selectors occurring in the tidal water–land boundary*

Type	Natural selectors	Selectors put into practice by man
Upwards		
Elevation	Island formed by accretion of silt, sand, etc. in tidal streams; shallow; shoal	Terp; dwelling mound; refuge for man, cattle and harvest during high water
Threshold	Shore-, beach-, creek-, river-bank, sand-bar, range of dunes, spit, ripple mark	Embankment, dike, sea-wall, flood-control dam, weir, barrage, groyne, jetty, breakwater
Downwards		
Depression	Basin in a salt marsh, river basin, catchment area, lake pond, pool, blowout	Drinking pool, port, harbour, dock, lock-chamber, flood storage basin,* excavated bottom-land
Channel	Watercourse, tidal channel, creek, dune valley	Trench, field-drain, drainage-furrow, ditch, canal, culvert
Intermittent		
Valve	Periodic alternation of ebb and flood	Sluice, tide-gate, lock-gate, dock, dike-burst
Interstitial		
Filter	Separation of the finer particles of mineral and organic material from the coarser ones; separation of organic material owing to difference in the manner and capacity of floating	Separation of areas with tidal or with non-tidal vertical water movements, and with predominantly salt or fresh water; seepage phenomena; permeability of field-drain pipes

* A reservoir filled during flood and emptying through a sluice during low water, constructed for cleaning of a tidal channel and preventing mud accumulation.

building a dike requires clay which leads automatically to cutting a ditch parallel to the dike. This close relationship between excavation and dike-building has its parallels in nature. For instance in the tidal marshes, creek beds representing 'accumulations of erosion' run parallel to the elevated creek banks, representing accumulations of sedimentation.

This feature manifests itself too in language. Niermeyer (1958) pointed out that the word 'dike', occurring in Sanskrit as 'dehî', means 'dike' as well as 'watercourse'. In Anglo-Saxon these two meanings are differentiated similarly, so that the word 'dîc' in its female form means 'ditch', and in its male form corresponds with 'dike'. Old Dutch toponyms make clear that in the Netherlands this word was also in vogue in these two significations.

This close vernacular relation with selectors discussed above in agricultural and communication sectors is also shown in several local family-names (Meertens 1947). Some striking examples are Hollestelle (a mound built to protect a fresh water-hole from pollution by unusually high tides) and Verheule (a 'heule' was originally a wooden bridge over a watercourse, later an arched brick-built bridge).

To protect the dike constructions against wave action, mats of straw were pegged down against the dikes. Later, facings of piles and pile-plankings were used. From 1731, however, the ship-worm (*Teredo navalis* L.) began to settle in this timber-work, and man had to change to costly revetments of limestone, granite and basalt, obtained from abroad, and extending from the foot of the dike to a metre or more above the average high water level at springs. The introduction of osier mattresses loaded with stones, and the use of underwater groynes to prevent sublittoral erosion, also date from these times. Today, particularly since the flood disaster of 1 February 1953, several new materials are used, for instance concrete, mine waste stones, asphalt and plastics.

So, living closely to his natural environment, medieval man thought, spoke and operated in terms of the water–land boundary. Especially at first he differentiated the landscape through small-scale operations and creation of derivative elements with natural materials either present or introduced. In modern times, however, his levelling influences, always present in principle, predominate more and more, especially as a result of scale-enlargement. In the south-west Netherlands these levelling influences will assume maximal dimensions in the realization of the so-called 'Delta Project'. This project aims to close the estuaries of the Rhine, Meuse and Scheldt except the Western Scheldt and the artificial Rotterdam Waterway, as well as to raise the remaining old sea dikes still serving as primary defence against flooding of the land behind them (Lingsma 1966; Lambert 1971).

In this context the recent pollution of soil, water and air by the use of fertilizers and pesticides in agriculture, by domestic effluents, and by discharge of industrial wastes is of outstanding importance, but falls outside the scope of this paper.

ECOLOGICAL SIDE-EFFECTS OF RECLAMATION MEASUREMENTS AND THEIR BEARING ON THE VEGETATION

The nature of the ecological side-effects of reclamation measures in coastal ecosystems can be considered from the view-point of 'stability' and 'instability' *sensu* van Leeuwen (1966). Stability is then defined as continuity in the existing situations and processes inherent in the nature of the ecosystem, while instability involves changes not intrinsic in that nature. For instance, when beach plains are gradually cut off from the tides by the formation of dune ridges this must be regarded as a natural process not interfering with inherent stability, in contrast with embanking where instability is abruptly introduced. Although each modification and intervention by man in itself increases instability, the time taken by these modifications, as well as the lifetime of their results, may introduce some, or sometimes even a good deal of stability. So we have to distinguish between positive side-effects, increasing the number of ecological niches through creation of ecoclines, and negative side-effects, decreasing ecological variety-in-space and enlarging contrasts-in-time, and thus creating ecotones. Frequently, both types of side-effects are coupled. For instance, embankment draws ecological contrasts together, but seepage of salt water through the dike, and propagation of tidal pressure waves in the ground water underneath, may establish complex gradient situations between the contrasts salt and fresh, wet and dry, periodic (tidal) and episodic (climatic) vertical water movements.

Negative ecological side-effects

Essentially, embankment initiates a complex of negative ecological side-effects. As already mentioned, it creates convergent environmental situations, drawing ecological contrasts together. It, too, intensifies the contrast between environments in which mineralization of organic soil material predominates, and those in which humification prevails. Mineralization is more important under the basic, and wet to humid tidal conditions; humification, on the contrary, is favoured in the more stable, decalcified soils of semi-natural grasslands on the inside of the dike. For example, under the polyhaline tidal conditions of the Scheldt Estuary grassland soils with 27% clay particles smaller than 2 μm contain about 10% humus, whereas in the saline soils of a small, eighty-year-old, neighbouring polder, 20% humus is found at the same clay content.

Outside the sea-dikes

Besides pushing ecological contrasts together, embankment favours instability, created either by nature or by man, on both sides of the dike. Outside, in the tidal region, it leads automatically to increase of uniformity of living conditions by:

(1) decapitating the catchment areas of creeks, especially those including higher grounds such as dunes;

(2) preventing discharge of rain water from the higher areas into the water–land boundary, except through sluices;

(3) narrowing the estuarine waterways which results in an increase of the tidal currents and of the flood levels through wedge storage, as well as of the range of the alternating brackish water-body;

(4) preventing expansion of the tidal marshes as a result of deepening of the waterways either naturally, in consequence of the narrowing process, or artificially for navigation purposes. Impermeable groynes or breakwaters, built as a defence against these deepening processes, often induce further erosion of the underwater foreshore.

All this has important consequences for the vegetation. Firstly, the decreased influence of fresh water on the tidal salt marshes results in species, largely confined to special gradient conditions between salt and fresh, becoming relatively rare, e.g. (see also Table 2):

Juncus gerardii	*Trifolium fragiferum*
Armeria maritima	*Lotus tenuis*
Carex extensa	*Ononis spinosa*
Scirpus rufus	*Odontites litoralis*
Agrostis stolonifera var. *salina* J. & W.	*Carex punctata*
	Alopecurus bulbosus
Carex distans	*Ranunculus sardous*
Leontodon autumnalis	*Taraxacum maritimum* Hgd., v. S. & Zb.

The first four species—*Juncus gerardii*, *Armeria maritima*, *Carex extensa* and *Scirpus rufus*—characterize communities of the higher salt-marsh alliance Armerion maritimae. The other species are characteristic of the provisionally defined group of salt-tolerant or obligatory brackish vegetation types classified in the Agropyro-Rumicion crispi (suballiance Loto-Trifolion). *Cochlearia anglica*, in the Wadden Area faithful for the

Table 2. *Some communities from the transition zone between the Armerion maritimae and the Agropyro-Rumicion crispi (upper salt marsh); beach plains of the Kwade Hoek, Goeree; 9 September* 1959

Number of relevé	1	2	3	4	5	6	7	8	9
Area (m²)	1×4	2×3	2×3	2×3	1·5×3	2×4	3×4	2·5×4	3×7
Cover of phanerogams (%)	95	98	100	100	100	98	100	100	100
Character-taxa of the Armerion maritimae									
Aster tripolium	03	r	r	r	–	–	r	–	–
Glaux maritima	p	p	a	a	a	r	r	r	–
Juncus gerardii	r	01	08	08	06	02	03	02	01
Plantago maritima	–	–	–	r	–	p	a	r	r
Festuca rubra f. *litoralis* Hack.	–	–	–	–	–	04	04	03	03
Character-taxa of the Agropyro-Rumicion crispi									
Juncus maritimus	06	p	r	r	r	r	p	r	–
Potentilla anserina	02	04	04	02	01	a	p	r	a
Plantago major	–	p	p	01	a	p	r	r	r
Odontites verna ssp. *serotina*	–	p	–	a	01	a	01	a	p
Lotus corniculatus	–	–	–	r	a	01	01	04	03
Trifolium fragiferum	–	–	–	–	–	r	r	r	p
Leontodon autumnalis	–	–	–	–	–	r	–	r	r
Carex distans	–	–	–	–	–	–	r	p	r
Other taxa									
Phragmites australis	01	01	a	a°	a°	a°	a°	a°	a°
Scirpus maritimus	a°	m°	r°	r°	r°	–	–	–	–
*Agrostis stolonifera**	–	05	p	a	02	02	02	01	02
Sonchus arvensis	–	–	r	–	–	r	r	r	p
Althaea officinalis	–	–	–	r°	a	p	–	–	–
Elytrigia pungens	–	–	–	–	r	p	r	a	02
Centaurium littorale	–	–	–	–	–	–	r	–	p
Leontodon nudicaulis	–	–	–	–	–	–	r	–	r

Additional taxa: Rel. no. 1: *Atriplex hastata* r°; Rel. no. 2: *Carex serotina* ssp. *serotina* r, *Centaurium pulchellum* r; Rel. no. 6: *Triglochin maritima* r, *Centaurium pulchellum r*; Rel. no. 8: *Mentha aquatica* a, *Sonchus asper* r, *Taraxacum* sp. r, *Leptodictyum riparium* (Hedw.) Warnst. r; Rel. no. 9: *Poa pratensis* p, *Hippophaë rhamnoides* p°, *Ononis spinosa* r, *Plantago coronopus* r.

Estimation of cover–abundance according to Doing Kraft (1954)—characters: cover always less than 5%, r = 1–3 individuals, p = 4–15 individuals, a = 16–40 individuals and m > 40 individuals; numbers: 01 = cover 5–15%, 02 = 15–25%, etc., 09 = 85–95% and 10 = 95–100%. Circles as exponents indicate reduced vitality.

* Partly var. *salina* J. & W. (character-taxon of the Agropyro-Rumicion crispi).

Armerion maritimae communities, probably occurred also in some parts of the Zuyderzee before its embanking in 1932, and in the mouth of the Rhine–Meuse estuary before its industrial occupation (van der Maarel 1962). Also a number of annuals, shuttling within these gradient situations from year to year, are relatively scarce (see Table 3):

Halimione pedunculata	*Centaurium pulchellum*
Parapholis strigosa	*C. littorale*
Sagina maritima	*Juncus bufonius*
Hordeum marinum	ssp. *ambiguus* (Guss.) Sch. & Thell.
Cochlearia danica	*Bupleurum tenuissimum*

Except *Halimione pedunculata* these species are characteristic for or related to communities of the Saginion maritimae. Some mosses, such as *Pottia heimii* (Hedw.) Fuernr. and *Amblystegium serpens* B. & S., also belong to this group. On natural localities they occur almost exclusively where freshwater habitats of dune or Pleistocene formations link with sandy or silty marshes.

Some of the species mentioned above, however, may persist locally on the outer slopes of the sea-dikes, thus showing at the same time a positive side-effect of embankment. As a rule, however, the construction of modern stone revetments, as well as the high amounts of tidal drift deposited against the dike faces—considerably increased through development of vast areas of *Spartina townsendii* s.l.*—prevented settlement of many of these species.

Secondly, the increase of instability, owing to narrowing and deepening of the estuarine waterways, promotes erosion with the result that many salt marshes show steep erosion edges in their faces. This feature is harmful for the settling of pioneers, such as *Zostera* spp., *Salicornia stricta* and *Spartina maritima*. Therefore, these species are rather rare, except in places where the tidal currents are slow. Contrary to the situation in the Wadden Area, *Zostera marina* is confined to the eulittoral zone in the south-west Netherlands and has been since the first half of the nineteenth century and probably earlier, because it was never found rooted in sublittoral substrates, either by fishermen or by botanists (J. G. Sloff, personal communication). In the Wadden Area *Z. marina* covered 15 000 ha of the partly sublittoral shallows before the epidemic of 1932–4 (van Goor 1919). The situation in the south-west Netherlands must be ascribed to violent tidal currents and to the absence of relatively stable shallows in the regions with tidal watersheds. The same holds for *Ruppia maritima*. Outside the dikes this species is found only locally on mud flats in the basin of the Eastern Scheldt and in tidal marsh pools in the Eendracht.

Known as promoting accretion more than other halophytic pioneers, *Spartina townsendii* was introduced from southern England in 1924–5, and planted in several localities. From there it disseminated spontaneously throughout the estuarine area, forming dense populations. Stabilizing many hectares of formerly shifting mud flats, and invading several tidal marshes, it has turned erosion of many foreshores into accretion. Nevertheless, this taxon, originated in recent times, acts ecologically as 'a stranger', and hence as a disharmonic element in the ecosystem. In the present situation it creates its own niche by disturbing both zonation and succession.

S. townsendii superseded the zonation on the mud flats, ousting the *Salicornia stricta* and *Spartina maritima* communities and, on the lower salt marshes, the greater part of

* Hubbard (1968) distinguishes the sterile hybrid *Spartina* × *townsendii* H. & J. Groves and the fertile amphidiploid *S. anglica* C. E. Hubbard derived from the primary hybrid by doubling of the chromosomes. As both sterile and fertile plants are found in the south-west Netherlands, both taxa probably occur; they both interfere with succession similarly.

Table 3. *Sequence of communities in the transition zone from salt marsh to dune formation, with development of character-species of the alliances Agropyro-Rumicion crispi and the Saginion maritimae; Kwade Hoek, Goeree;* 8 *September* 1959; *for explanation of the cover–abundance symbols see Table* 2, *p.* 430

Number of relevé	1	2	3	4	5	6	7	8	9	10	11	12	13
Area (m^2)	1·5×3	1·5×5	2·5×4	4×5	3×6	2×5	2×8	2×8	4×6	2×6	4×6	2·5×8	2×4
Cover of phanerogams (%)	70	85	95	100	100	100	95	85	70	85	95	95	98
Cover of cryptogams (%)	–	–	–	–	–	–	5	10	20	20	30	20	3
Level of soil surface relative to Rel. no. 1 (cm)	0	4	9	13	22	25	30	35	40	36	30	25	20
Character-taxa of the Glauco-Puccinellietalia (excl. Armerion)													
Suaeda maritima	r°	r°	–	–	–	–	–	–	–	–	–	–	–
Salicornia europaea	p°	p°	–	–	–	–	–	–	–	–	–	–	–
Triglochin maritima	a	p	p	–	–	–	–	–	–	–	–	–	–
Spergularia marina	a°	02	r	–	–	–	–	–	–	–	–	–	–
Aster tripolium	p°	p°	a°	p°	–	–	–	–	–	–	–	–	–
Puccinellia maritima	05	04	r	r	–	–	–	–	–	–	–	–	–
Character-taxa of the Armerion maritimae													
Glaux maritima	02	03	02	01	a	p	–	–	–	–	–	r°	r°
Plantago maritima	r	r	02	01	a	a	p	p	p	r	a	01	a
Juncus gerardii	–	a	05	03	04	02	–	–	–	–	–	03	04
Artemisia maritima	–	–	r	–	–	r°	–	r°	p	–	–	–	–
Festuca rubra f. *litoralis*	–	–	p	04	05	03	03	r	a°	p°	a°	04	04
Character-taxa of the Agropyro-Rumicion crispi													
Trifolium fragiferum	–	–	–	r	p	r	r	–	–	–	–	–	–
Ononis spinosa	–	–	–	r	r	p	p	p	a	r	r	–	–
Leontodon autumnalis	–	–	–	–	r	p	a	–	–	–	–	–	–
Lotus corniculatus	–	–	–	–	r	r	r	r	–	–	–	–	r
Odontites verna ssp. *serotina*	–	–	–	–	r°	r	r	r°	r°	–	–	–	–
Trifolium repens	–	–	–	–	r	r	r	–	r	r	r	r	p
Poa pratensis	–	–	–	–	–	p	02	a	a	p	p	–	–

Table 3 (*contd*)

Number of relevé	1	2	3	4	5	6	7	8	9	10	11	12	13
Character-taxa of the Saginion maritimae													
Bupleurum tenuissimum	–	–	–	r	p	a	m	m	p°	a	a	m	a
Plantago coronopus	–	–	–	–	–	r	p	01	01	a	r	r	r
Sagina nodosa	–	–	–	–	–	–	–	p	a	a	–	–	–
S. maritima	–	–	–	–	–	–	–	a	a	m	m	a	–
Character-taxa of dune associations													
Leontodon nudicaulis	–	–	–	–	–	–	r	p	p	r	r	–	–
Sedum acre	–	–	–	–	–	–	r	01	m	m	a	–	–
Eryngium campestre	–	–	–	–	–	–	r	–	p°	r	–	–	–
Bryum angustirete Kindb.	–	–	–	–	–	–	p	p	a	02	03	02	a
Galium verum	–	–	–	–	–	–	–	p	p	–	r°	–	–
Eryngium maritimum	–	–	–	–	–	–	–	r°	a	r°	–	–	–
Honckenya peploides	–	–	–	–	–	–	–	–	p°	p°	–	–	–
Tortula ruraliformis Dixon	–	–	–	–	–	–	–	–	01	r	r	–	–
Other taxa													
Elytrigia pungens	–	–	–	–	a	03	04	06	06	06	07	a	r
Taraxacum sp.	–	–	–	–	r°	r°	p°	p	p	p	–	r	–
Barbula convoluta Hedw.	–	–	–	–	–	–	01	01	p	p	–	p	–
Brachythecium albicans B. & S.	–	–	–	–	–	–	–	p	p	r	–	–	–

Additional taxa: Rel. no. 3: *Atriplex hastata* r°, *Spergularia media* r; Rel. no. 7: *Cirsium vulgare* r; Rel. no. 8: *Cerastium* sp. r°, *Cochlearia danica* r°; Rel. no. 9: *Ammophila arenaria* r, *Hypochaeris radicata* r; Rel. no. 10: *Cerastium* sp. p; Rel. no. 12: *Sonchus oleraceus* r°.

the Puccinellietum maritimae communities, except for the less silty habitats (Beeftink 1965). This process is still going on in the south-west Netherlands.

In succession *S. townsendii* seems to be unsuccessful, at least under euhaline and polyhaline conditions (Fig. 2). There are strong indications that under those salinity conditions *S. townsendii* communities—if not embanked in the meantime—are incapable of fitting in the natural succession series of the salt-marsh vegetation. In the polyhaline Southampton Water where more than half-a-century-old *Spartina* meadows are found, serious 'die-back' phenomena broke out (Goodman, Braybrooks & Lambert 1959; Goodman 1960; Goodman & Williams 1961; Bird & Ranwell 1964), followed by extensive erosion and cliff formation. Over large areas—according to Hubbard (1965) in Poole Harbour about 20% of its maximal surface—*S. townsendii* appeared to be 'worn-out', without being succeeded by other halophytes. This collapse may point to incompatibility between the soil conditions created by this *Spartina*, and the salt-marsh species which might have been expected to have settled as successors of *Spartina* considering the level

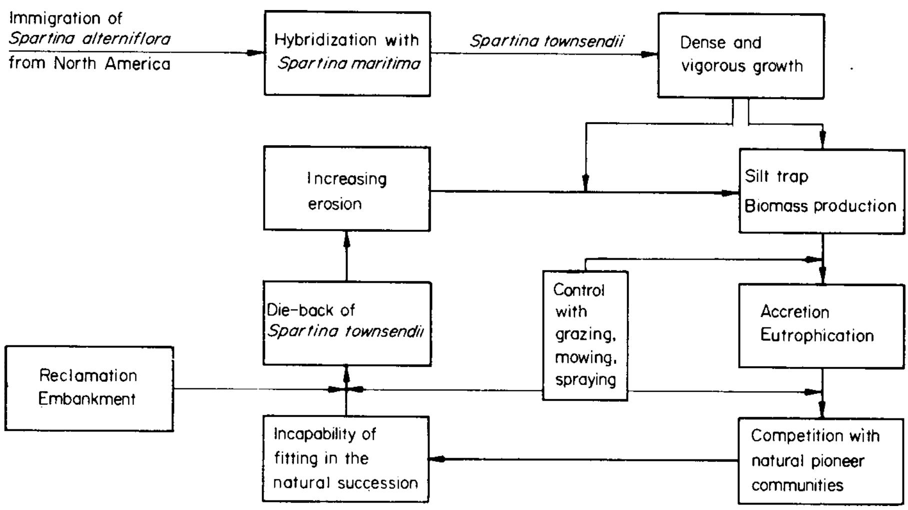


FIG. 2. Disfunction of the introduction of *Spartina townsendii* in the salt-marsh ecosystem of eu- to polyhaline waterbodies.

to which the soil has been accreted with respect to the tides. Apparently, these *Spartina* meadows turn back to the originally shifting mud flats and thus give an ecological illustration of the proverb 'easy come, easy go' (van Leeuwen 1966; van Leeuwen & van der Maarel 1966). Similar developments have not been observed in the Netherlands but the *S. townsendii* vegetation here is of recent date.

In the mesohaline Bridgwater Bay, however, Ranwell (1961, 1964a, b) found that grazing pressure and accumulation of *Spartina* litter deposited by the tides at the top of the *Spartina* marsh facilitated the invasion of higher-marsh species. Thus, it seems that under more estuarine circumstances than in Southampton Water the accumulated stress conditions have a levelling influence on the incompatibility phenomena, either by forcing *Spartina* to give up its territory in favour of other brackish-marsh species, or by preparing soil conditions compatible for successors.

Further levelling influences on coastal marsh vegetation by man are surface drainage works and measures promoting accretion. In former times, till about half a century ago,

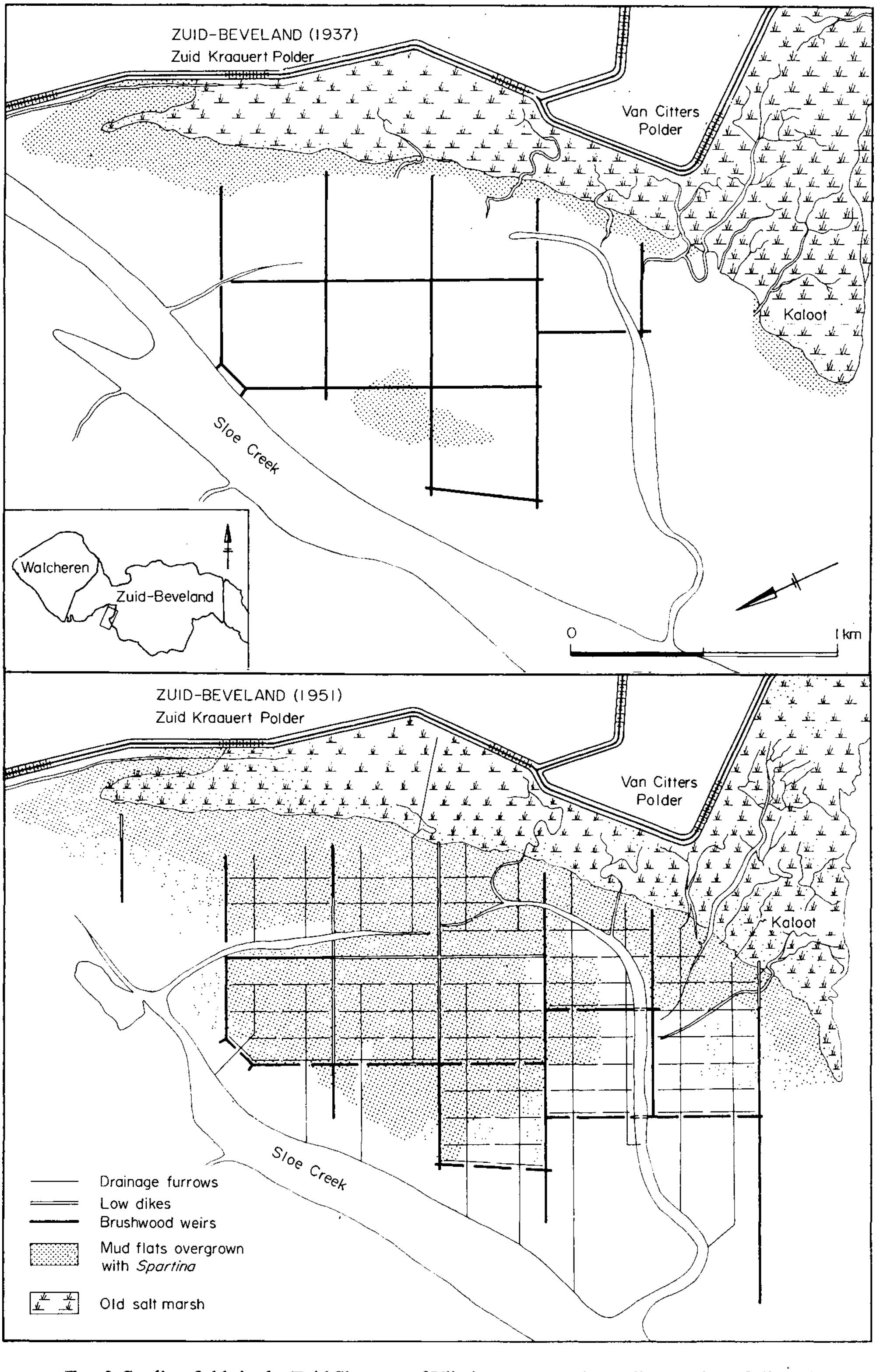


FIG. 3. Settling-fields in the Zuid Sloe east of Vlissingen promoting sedimentation of silt and the increase of *Spartina townsendii* from 1937 to 1951. Maps published by kind permission of the 'Dienst der Domeinen' (Public Lands Department, South-west Holland Inspectorate).

man cut trenches mostly perpendicular to the dike to promote drainage and a more uniform accretion. In the salt and brackish marshes of the Wadden Sea and the Rhine–Meuse estuary these trenches can still be seen. In the south-west Netherlands trenching was done—and is locally still done—for the benefit of reed, bulrush and brushwood culture. Moreover, shepherds, living close to nature, promoted the development of well-defined vegetation types, such as communities of *Puccinellia maritima* by local drainage. Large-scale drainage leads automatically to levelling of the soil surface, and thus to a decrease of the spatial environmental diversity. Owing to the uniformity in distance and water-carrying capacity of the drainage-furrows the natural watercourses lose their function and fill up, and the basins will silt up. Other measures applied for promoting accretion and outbuilding of the marshes are the construction of settling-fields for mud and silt by means of weirs of brushwood and other slow-weathering material. In recent times these weirs were placed in squares with gaps at the seaward side, as in the Zuid Sloe near Vlissingen (Kalkwijk 1954). When the mud surface rose to above 1 m below Mean High Water, *Spartina townsendii* was planted (Fig. 3). These, and other similar plantations, lead to the development of vast monotonous communities.

In the estuary as a whole, narrowing the waterways by embankment intensifies the degree of environmental instability through increase and further ingression of the tides owing to the increase of depth of the tidal channels. This deepening is manifest (1) in an increased wedge storage, pushing the tidal waves further upstream against the discharge of the river, (2) in greater salinity fluctuations extending over longer ranges and (3) possibly in a higher accumulation of suspended solids—inorganic as well as organic—intensified by flocculation and deflocculation processes induced by the greater fluctuation of salinity.

In estuaries there is a positive relationship between the distance the salt-water wedge extends upstream from Low Water Springs to the next High Water Springs (van Veen 1954), and the third power of the maximal depth of the tide channel when the upstream carrying-capacity remains unchanged (van der Burgh 1968). Moreover, the narrowing of the estuarine cross-section area by embankment leads automatically to deepening of the waterway because the cross-section area tends to preserve its surface. Thus man has induced considerable ingression of the salt wedge in tide channels. Consequently the salinity fluctuations in the tidal water, and in the soil moisture of the marshes, extend more deeply into the estuary.

Estuarine instability also promotes the development of tidal marsh phytocenoses with a single or a few dominating species. Their pattern of distribution appears to fit very well with the convergent phenomena, particularly with those of instability in salinity fluctuations. In the mesohalinicum, where this instability reaches its maximal values with respect to benthic organisms, the total number of phanerogams in the tidal marshes is minimal. In this zone, too, dominance is more pronounced in the supralittoral belt, as is shown by some of the more euryhaline species such as:

Aster tripolium	*Festuca rubra* f. *litoralis* Hackel
Agrostis stolonifera var. *salina* J. & W.	*Elytrigia pungens*
Puccinellia maritima	

Seaward, in the poly- and euhalinicum the salt-marsh vegetation is reinforced by the less euryhaline halophytes:

Salicornia europaea agg.
Suaeda maritima
Halimione portulacoides
Limonium vulgare
Spergularia media
Artemisia maritima
Armeria maritima

In the reverse direction one finds many riparian species ending their area of distribution downstream in the oligohalinicum and the adjacent part of the mesohalinicum (Fig. 4).

Although most of the less euryhaline halophytes mentioned above seem to be confined to fixed levels with respect to the tides, several of the more euryhaline species show the phenomenon of submergence in the brackish environment (Remane 1950, 1955, 1958), descending from the supralittoral part above Mean High Water Springs to that under Mean High Water Springs, and in some cases even down into the upper part of the eulittoral zone. Species exhibiting increasing submergence are (Beeftink 1965):

Spergularia marina
Puccinellia distans
Glaux maritima
Juncus gerardii
Agrostis stolonifera
Spartina townsendii
Atriplex hastata

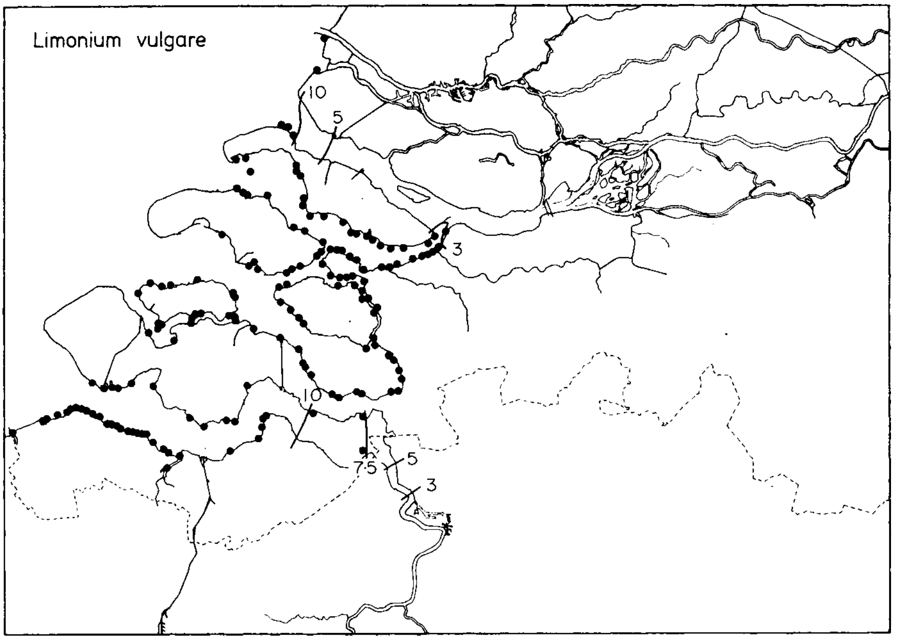
On the other hand, but in reverse direction, many riparian species, originating from the fluvial area, penetrate downstream into the brackish environment, wedging out on gradually higher levels. These species show the feature of emergence (Remane 1958). Among them are the following species:

Galium aparine
Solanum dulcamara
Rumex obtusifolius
Symphytum officinale
Cirsium arvense
Festuca arundinacea
Angelica archangelica
Cerastium holosteoides
Polygonum amphibium
Phragmites australis
Scirpus maritimus

These patterns of limits, descending from marine to freshwater environment, result in a zone with an absolute species minimum descending in the same direction through the supralittoral and upper eulittoral belts. Likewise, upstream the maximal fluctuations in soil-moisture salinity shift gradually to lower levels in a similar way to those of the estuarine water (Beeftink 1965).

It was emphasized above that embankment promotes instability of salinity fluctuations over a longer range. From this point of view it can be concluded that, conversely, under unembanked circumstances the instable transition zone between sea- and river-water will generally extend over a shorter estuarine range and will have less tidal fluctuations, owing to flood absorption by a larger surface/content ratio of the tidal waterway. Under those completely natural circumstances instability originating from tidal and salinity fluctuations must be more limited in the longitudinal direction, but more extended in the transverse direction with respect to the tide channels. The same must hold for the area of distribution of the species limited to that instable transition zone, such as (Fig. 4):

Althaea officinalis
Cochlearia officinalis
Apium graveolens
Oenanthe lachenalii
Ranunculus sardous
Alopecurus bulbosus
Taraxacum maritimum Hgd., v. S. & Zb.
T. intermedium Raunk.
T. olitorium Hagl.
Triglochin palustris
Samolus valerandi



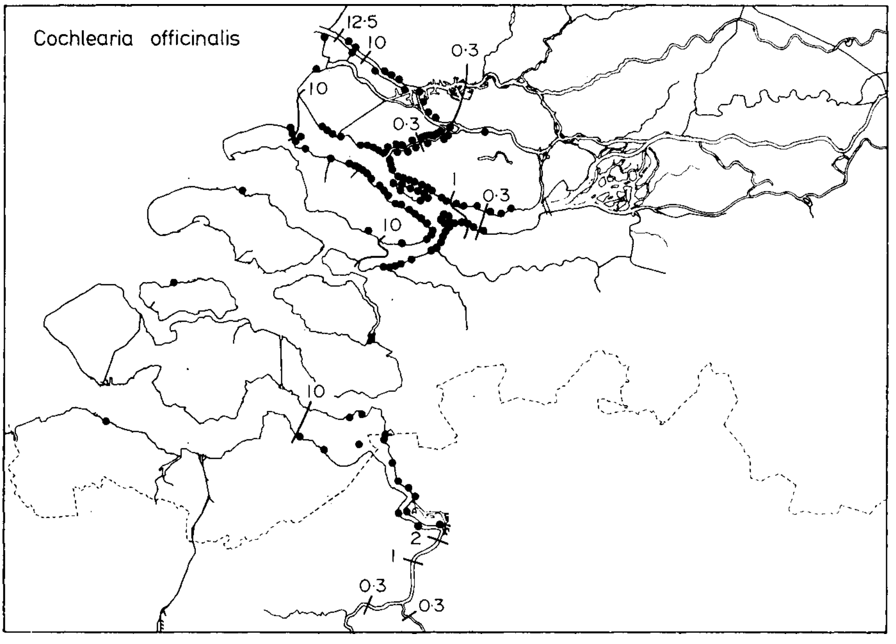


FIG. 4. Examples of the estuarine distribution of a less euryhaline plant species (*Limonium vulgare*), a more euryhaline one (*Aster tripolium*), a species limited to brackish conditions (*Cochlearia officinalis*), and a glycophytic (riparian) species (*Caltha palustris*). Distribution patterns in relation to isohalines (chlorinity in ‰) at tidal high-water levels and average river discharge.

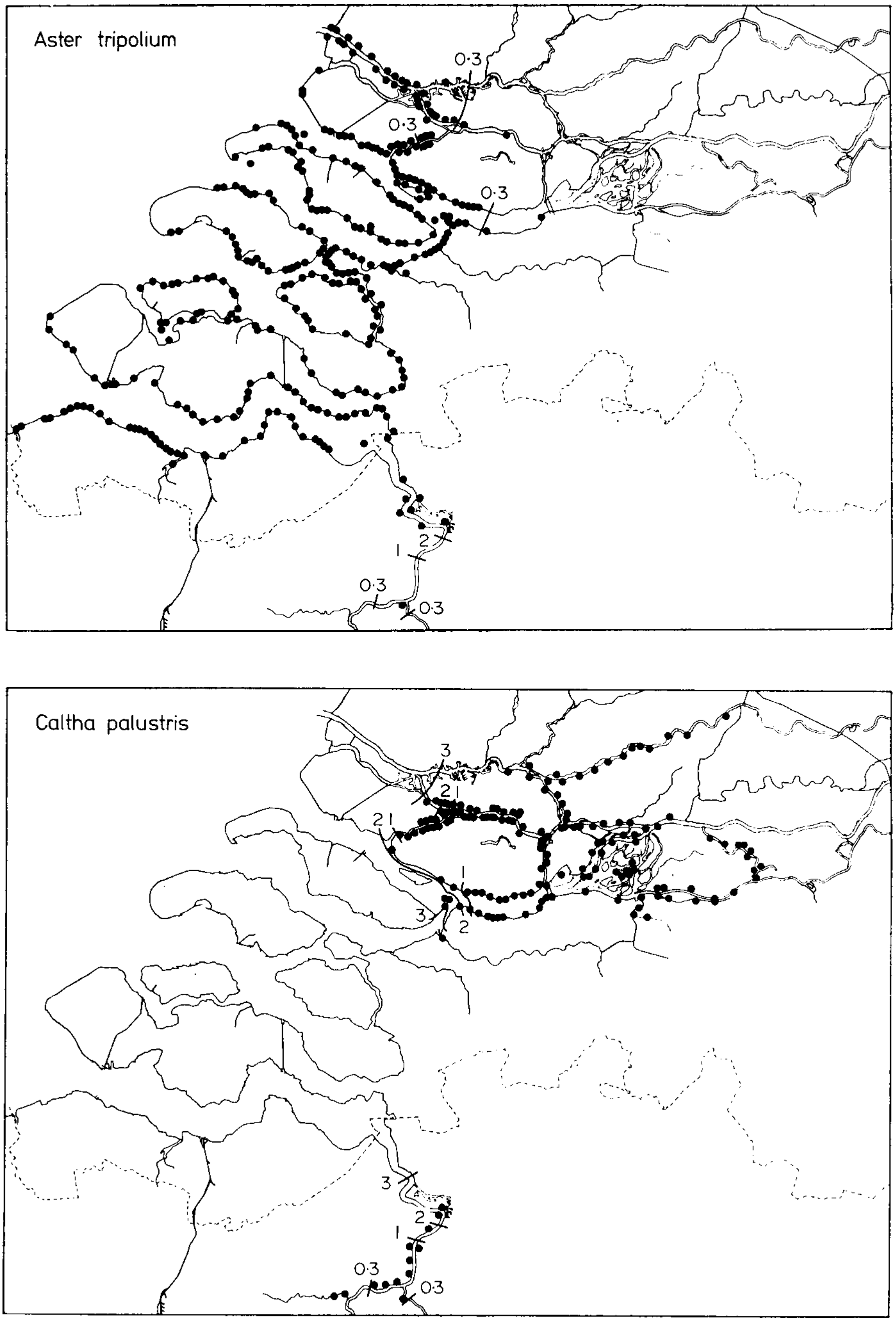

Aster tripolium
0·3
0·3
0·3
2
1
0·3
0·3
Caltha palustris
3
2 1
2 1
1
3
2
3
2
1
0·3
0·3

FIG. 4 (*contd*)

Inside the sea-dikes

In the primitive polderland, negative ecological side-effects of embankment are evident as well. In the first place the dominating periodic vertical tidal movements were changed into episodic ones dependent on climatic irregularities. To reclaim this newly created temporarily waterlogged and partly inundated polderland, a primitive field-drainage system was built, carrying off the surplus of rain- and seepage-water through sluices. In many places, however, drainage impeded the leaching of the excess salts to an admissible level for agriculture, and admitted the saline ground water to move upwards. In this way both climatic irregularities and the continuing rise in sea-level upheld instability in hydrology and salinity. In several places, especially in the low-lying peaty areas of the old island nuclei, there is still instability.

Owing to these conditions large parts of the older polder areas could be used only for animal husbandry. Especially in connection with the wool-industry centres in Flanders, sheep were attractive in these areas (Gottschalk 1955). Under such conditions varied Agropyro-Rumicion crispi communities are apt to spread over nearly the whole grazed area. At the same time the halophytic vegetation retreated in and on the borders of saline relicts such as sloughs, bottom land creeks, brackish peat soils, and salinized cattle tracks.

Since their formation these instable grasslands have also provided suitable feeding grounds for large quantities of wintering geese, notably when situated within reach of isolated tidal marshes used as roosting places (Webbe 1958; Lebret 1959).

Studying the ecology of *Limnaea truncatula* (Müller) as an intermediate host of *Fasciola hepatica* (L.) (liver fluke disease), Over (1967) emphasized that holes poached by the effect of cattle greatly reduce the risk that whole populations of this mollusc will become extinct. Such holes will mainly be found near the drainage-furrows, in the case of controlled intensive grazing as the cattle will avoid this wet, waterlogged zone when not compelled to graze there. In this way rapid recolonization and build-up of dense populations of the mollusc is guaranteed. It was thus demonstrated that besides the generally recognized relationships cattle–parasite and mollusc–parasite, the relationship cattle–mollusc exists as well owing to the way the water–land boundary is managed.

Honer (1963) investigated more deeply the problem of the influence of the characteristic landscape structure of the Netherlands on the ecology of diseases caused by larval trematodes. He stated that the process of 'poldering' characterized by its prevalent ditch and drainage-furrow system together with its side-effects, such as seepage with fresh to more or less salt water, must be considered to give rise to an ecotone or 'stress-zone'. The watercourses and adjacent marshy or soggy spots in the field, where the biota are constantly exposed to stress conditions, must be seen as potential habitats for trematodes. From this point of view the habitat, suitable for the existence of the trematodes and their hosts, has been greatly extended by human influence. At the same time the process of 'poldering' created large amounts of open water surfaces, some of them covering vast areas in winter attracting large numbers of waterfowl, the main hosts of various trematodes. This arrangement of the landscape for both groups of warm-blooded hosts appeared to involve the creation of habitats suitable for the intermediate (molluscan) hosts and thus a risk-reducing system for the trematodes was created. In this way the process of 'poldering' had and still has a levelling influence and a negative ecological side-effect.

Positive ecological side-effects

As already mentioned, former embankments affected the vegetation in many positive ways. While the impact of negative side-effects is mainly found outside the dike, the positive side-effects are usually felt in the polderland. These positive effects are generated by the dike itself, by local lowering of the land surface through shrinking of the peat layers, by superficial mining activities, and local differences in drainage control and farming management. These former human activities together with the (semi-) natural environmental processes originated from them, created a varied spatial diversity in the polderland, resulting in a varied vegetation cover. This diversity comprises particularly spatial differences in (1) the period elapsed since the land was protected from flooding, (2) the level of the soil surface and the ground-water table, (3) the fluctuation of the ground-water level and its salinity and (4) the use by man.

Together with natural and artificial watercourses the dike forms the most pronounced element as to difference in level. While the slopes of the watercourses represent the wetter and cooler aspects of the gradient situation—but complicated by flooding and eutrophication—the dike represents the drier and partially warmer aspects. Ecologically the dikes form most interesting tracks for plant migration between the elevated habitats of salt marshes, dunes and rocky coasts on the sea-side, and 'river-dunes' (see p. 453) and terraces in the river-valleys on the fluvial side. Among the dikes three types can be distinguished: (1) the sea-dikes, principal defenders, extending from the sea-coast into the fluvial region embanking the winter-beds; (2) the summer-dikes, for the most part extending into the fluvial region embanking the summer-beds of the rivers; and (3) the retired embankments as second or subsequent lines of defence.

The meaning of reduced flooding, seepage and dike-bursts for plant growth

Each type of dike has its own capacity and function in excluding tidal influences. The summer-dikes, thrown up in front of the sea-dikes proper, are lower and overflow during storm floods and high river discharge. They return the flood-water through outlets with a one-way sluice valve. Summer-dikes were constructed nearly everywhere in the fluvial region and in the freshwater tidal zone, but are rather scarce in mesohaline parts of the estuaries, and even rarer in the polyhaline zone. In the last zone the grassland between summer- and winter-dike forms a habitat intermediate between the saline tidal environment outside the dike and the mainly fresh non-tidal habitat further inland. The halophytes and salt-tolerant species are growing at a lower level than in the salt marshes, thus demonstrating the intermediate character of the habitat. For instance the halophyte *Halimione portulacoides* (stunted form) is here not established on the banks of the natural creek remnants, but in basins and creek-beds which dry up in summer. Of the halophytic associations only the Puccinellietum distantis (characteristic for trodden sites), the Puccinellietum maritimae and the Juncetum gerardii are represented. The last association is usually intermingled with and even superseded by species characteristic of the alliance Agropyro-Rumicion crispi (Table 4). On the creek banks the Artemisietum maritimae and the Atriplici-Elytrigietum pungentis are replaced by communities in which *Hordeum secalinum* usually dominates, accompanied by *Lolium perenne*, *Trifolium repens*, *Taraxacum* Sectio *Vulgaria*, *Ranunculus sardous*, *Cirsium arvense*, etc. On the creekward sides of the banks the Halimionetum portulacoidis is replaced by *Ononis spinosa* communities, allied to the Ononi-Caricetum distantis. Further upstream, in the meso- and oligohaline zones, these communities develop outside the protecting summer-dike, but only if they are grazed. Here, and in the freshwater tidal zone the floristic difference between the grassland outside and inside the summer-dike corresponds more to differences in land use than to differences in frequency and duration of flooding.

The capacity of dikes as defences against the sea is hampered in three ways: (1) by seepage through and underneath the dike; (2) by leakage through sluices; and (3) by overflow and dike-bursts during exceptionally high storm floods or through suction scour by the tidal water in the underground. The first two limitations represent the filter type in Table 1, introducing some environmental divergence on the landward side. Dike-bursts, on the contrary, represent the valve type (Table 1) introducing instability. Owing to seepage and tidal pressure waves in the ground water, gradients in salinity and vertical periodic water movements are established within the polderland, with the result that locally weakened tidal fluctuations are found in the watercourses. In such situations many less euryhaline halophytes (*Limonium vulgare*, *Halimione portulacoides*, *H. pedunculata*, *Spergularia media* and *Artemisia maritima*) find suitable habitats. Inside the dike these species are even restricted to such places. As marshes mature, silt is deposited against the foot of the dike, the ground-water level rises, and seepage pressure will increase. It depends on the efficiency in draining the polder whether and to what extent the inland tidal fluctuations remain.

Besides seepage, leekage through sluices stimulates settlement of many halophytes on the bottom and slopes of ditches and other watercourses. *Ruppia maritima*, *Salicornia europaea* agg., *Suaeda maritima*, *Aster tripolium*, *Triglochin maritima*, *Glaux maritima*, *Juncus gerardii*, *Puccinellia maritima*, *P. distans*, *Spergularia marina* and several salt-tolerant Agropyro-Rumicion crispi species are often encountered in such situations. Polders flooded by dike-bursts may preserve their saline soils for decades, or perhaps even centuries, mainly in excavation sites, ponds and creeks, and thus halophytic communities fading into grassland communities of varying floristic composition are still found in the lower parts of the polderland. As the less euryhaline halophytes are usually lacking, these halophytic communities are poor in species if well-developed and not intermingled with salt-tolerant ones such as several Agropyro-Rumicion species. These communities show then also a more pronounced dominance of the remaining species.

The dike as a habitat for plant growth

The sea-dike shows large differences in structure, exposure, soil texture, human exploitation and age. In defending the sea-dike with stone revetments of different kinds down to the bottom even into the sublittoral zone, often with stone-loaded brushwood mattresses at its toe, man introduced new substrata. In this way biota requiring a solid substratum could settle along the coasts of the Netherlands, for example Hydrozoa, Bryozoa, sea-anemones, barnacles, algae, lichens, and even occasionally some phanerogams (*Crithmum maritimum*, *Beta maritima*, *Crambe maritima*). As den Hartog (1959) pointed out, the epilithic algal vegetation of the Wadden Sea must be of a more recent date than corresponding vegetation abroad. According to this author this vegetation is still expanding, many new species coming in since 1870. This continuous increase in algal species, doubtless also valid for other groups, demonstrates the importance of time, even in relatively instable environments, required by the biocenoses to obtain their maximal diversity. However, the use of new products of defence for modern dikes turns this gradual increase into a relatively rapid decrease. Asphalt especially appears to be disastrous (den Hartog 1959). Pollution and smoke from industry and navigation also lead to the extinction of several species.

The dike habitat shows complicated zones and sequences of relatively instable and stable aspects owing to its exposure to marine influences. Firstly the zonation of creek bank communities (Halimionetum portulacoidis and Artemisietum maritimae) normally

Table 4. *Sequence of plant communities in the low-embanked salt marshes on the south coast of the island of Goeree-Overflakkee; for explanation of the cover–abundance symbols see Table* 2, *p*. 430

Number of relevé	1	2	3	4	5	6	7	8	9	10	11	12	13
Date	4 Sept. 1969	21 Sept. 1970	23 June 1971	18 Sept. 1970	22 June 1971	19 Sept. 1968	23 June 1971	7 July 1965	19 Sept. 1968	23 June 1971	7 July 1965	7 July 1965	7 July 1965
Area (m^2)	1·5×3	1·5×4	2×3	2×4·5	2×3	1·5×4	2×5	1×5	1×10	1×6	4×9	3×8	4×8
Cover of phanerogams (%)	40	75	75	90	98	70	100	100	100	100	98	98	100
Character-taxa of the Glauco-Puccinellietalia													
Salicornia europaea agg.	02	01	–	p	p	–	–	–	–	–	–	–	–
Suaeda maritima	02	–	–	r	r	–	p	–	–	–	–	–	–
Spergularia marina	m	06	05	m	r	m	–	–	–	–	–	–	–
Puccinellia distans	–	–	03	–	–	a	–	–	–	–	–	–	–
P. maritima	p	01	p	09	07	01	–	–	–	–	–	–	–
Plantago maritima	r	–	–	–	r	–	01	a	–	–	a	–	–
Glaux maritima	–	r	–	r	01	02	01	03	p	–	m	r	r
Aster tripolium	–	a°	r°	a°	m°	–	m°	r°	r	a	a°	p°	–
Triglochin maritima	–	–	–	r	p	r	r	p	–	–	–	–	–
Halimione portulacoides	–	–	–	r°	–	r°	–	r°	–	–	r°	r°	–
Juncus gerardii		–	–	–	03	04	07	01	–	a	p	–	–
*Festuca rubra**		–	–		–	–	01	08	05	04	02	03	02

Table 4 (*contd*)

Number of relevé	1	2	3	4	5	6	7	8	9	10	11	12	13
Character-taxa of the Plantaginetalia majoris													
Agrostis stolonifera	–	–	r	–	r	r	01	02	03	01	05	02	02
Polygonum aviculare	–	–	p	–	–	r	–	–	r	–	–	p	–
Plantago major	–	–	–	–	r	a	–	–	r	r	r	r	–
Elytrigia repens	–	–	–	–	–	p	–	–	p	01	01	–	–
Potentilla anserina	–	–	–	–	–	r°	–	–	r	01	r	01	02
Leontodon autumnalis	–	–	–	–	–	–	m	–	a	a	r	p	–
Poa pratensis	–	–	–	–	–	–	p	–	–	01	–	–	–
Trifolium fragiferum	–	–	–	–	–	–	–	a	m	p	a	p	–
T. repens	–	–	–	–	–	–	–	p	a	p	p	p	a
Lotus tenuis	–	–	–	–	–	–	–	a	–	a	a	a	p
Taraxacum sp.	–	–	–	–	–	–	–	r	p	–	p	p	a
Ranunculus sardous	–	–	–	r	–	–	–	–	p	r	–	–	r
Lolium perenne	–	–	–	–	–	–	–	–	01	p	p	p	01
Taxa characteristic of communities on tidal drift													
Atriplex hastata	–	p°	m	p°	a	r	–	r°	–	–	a°	p°	r
Elytrigia pungens	–	–	–	–	–	–	–	–	–	–	–	a	p
Cirsium arvense	–	–	–	–	–	–	–	–	–	–	–	03	08
Taxa characteristic of dry grasslands													
Hordeum secalinum	–	–	–	–	–	–	–	r	a	01	03	03	03
Cerastium holosteoides ssp. *triviale*	–	–	–	–	–	–	–	–	p	r	–	–	–
Ononis spinosa	–	–	–	–	–	–	–	–	07	02	–	–	–

Additional taxa: Rel. no. 2: *Spartina townsendii* r°; Rel. no. 3: *Parapholis strigosa* p; Rel. no. 4: *Chenopodium rubrum* r°, *Plantago coronopus* r; Rel. no. 5: *Parapholis strigosa* m; Rel. no. 6: *Chenopodium rubrum* r; Rel. no. 7: *Armeria maritima* r, *Plantago coronopus* a, *Spergularia media* a; Rel. no. 8: *Eurhynchium praelongum* (Hedw.) Hobk. a, *Armeria maritima* r; Rel. no. 9: *Bellis perennis* r, *Plantago coronopus* r, *Stellaria media* r, *Urtica dioica* r; Rel. no. 10: *Bellis perennis* p, *Medicago lupulina* p; Rel. no. 11: *Armeria maritima* r, *Spergularia media* r.

* Mainly or entirely f. *litoralis*.

develops at the toe of the dike-faces in the eu- and polyhalinicum, thus proving the habitat to be ecologically similar to natural bank formations. Mostly, however, this original vegetation is suppressed by belts of plant debris washed ashore, and consequently replaced by dense populations of *Atriplex hastata* and *A. littoralis* (Atriplicetum littoralis) and turfs of *Elytrigia pungens* (Atriplici-Elytrigietum pungentis). It is supposed that in the last half century these nitrophilous species largely increased owing to the mass production of organic material by the vast areas of *Spartina townsendii* (Beeftink 1965). In the same way the composition of the flotsam belts became more uniform, as the amount of seaweeds is outmassed by the *Spartina* debris. The nitrophilous vegetation thus became floristically more uniform and poorer in species (for instance by a decrease of *Matricaria inodora* incl. *M. maritima*). On flotsam washed against stone revetments, besides the species mentioned above, mainly *Galium aparine*, *Sonchus arvensis* var.

Table 5. *Sequence of communities on tidal drift washed against the dike face; Eastern Scheldt near Rilland;* 4 *June* 1965; *for explanation of the cover–abundance symbols see Table* 2, *p.* 430

Number of relevé	1	2	3	4	5	6
Area (m²)	3 × 10	2 × 6	1 × 8	1 × 10	3 × 8	3 × 10
Cover of phanerogams (%)	40	40	50	80	100	100
Level of soil surface relative to Rel. no. 1 (cm)	0	20	40	90	120	180
Puccinellia maritima	r	–	–	–	–	–
Suaeda maritima	04	m	–	–	–	–
Halimione portulacoides	01	m	–	–	–	–
Festuca rubra f. *litoralis*	r	r	–	–	–	–
Aster tripolium	–	r	–	–	–	–
Atriplex hastata	a	03	01	p	–	–
A. littoralis	p	m	04	02	–	–
Elytrigia pungens	–	r	p	a	–	–
Sonchus arvensis var. *typicus* Beck	–	–	r	r	–	–
Galium aparine	–	–	m	07	01	p
Elytrigia repens	–	–	m	m	10	06
Rumex crispus	–	–	r	p	p	p
Matricaria inodora	–	–	–	p	r	–
Cirsium arvense	–	–	–	–	a	06
Arrhenatherum elatius	–	–	–	–	p	a
Urtica dioica	–	–	–	–	–	p

Additional taxa: Rel. no. 5: *Dactylis glomerata* r; Rel. no. 6: *Symphytum officinale* r.

typicus Beck, *Cirsium arvense*, *Rumex crispus* and sometimes *Calystegia sepium* and *Stellaria media* are found (Table 5). On flotsam in the meso- and oligohalinicum these species are more prominent, together with *Solanum dulcamara*, *Althaea officinalis*, *Sonchus palustris*, *Rumex obtusifolius*, *Epilobium hirsutum*, *Angelica archangelica*, etc. (classified in the alliance Angelicion littoralis, see Beeftink 1965).

Treading makes the sea-dike face a quite different habitat. Tracks, made by cattle or by man, usually run close above the stone revetment or the zone where most flotsam is deposited. The soil shows large fluctuations in moisture content combined with sharp rises and falls in salinity. In the polyhalinicum *Puccinellia distans* and *Spergularia marina* are characteristic (Puccinellietum distantis). On similar, but more continuously dry, occasionally splashed and mostly sandier soils, are often elements of the Saginetum maritimae, viz.

Table 6. *Sequence of communities with* Cynodon dactylon *occurring against the outer face of a 250-year-old sandy sea-dike protected against direct wave action; Preekhilpolder near Ouddorp, Goeree; 22 June* 1965; *for explanation of the cover–abundance symbols see Table* 2, *p.* 430

Number of relevé	1	2	3	4	5
Area (m²)	2×3	0·6×3	1·5×3	2×3	5×6
Cover of phanerogams (%)	95	95	95	100	95
Cover of cryptogams (%)	70	80	10	<1	<1
Character-taxa of the Glauco-Puccinellietalia					
Artemisia maritima	p	a	–	–	–
Juncus gerardii	01	a°	m	–	–
Festuca rubra f. *litoralis*	07	04	05	04	03
Armeria maritima	–	p	r	–	–
Character-taxa of the Plantaginetalia majoris					
Cynodon dactylon	a	04	02	02	r
Plantago coronopus	a	p	p	p	p
Leontodon autumnalis	p	r°	m	p	a
Lotus tenuis	a°	a	a	p	p
Trifolium repens	p°	–	a	01	a
Taraxacum sp.	p	–	p	p	p
Agrostis stolonifera	–	p	r	–	a
Lolium perenne	–	–	p	p	03
Poa pratensis	–	–	–	01	r
Elytrigia repens	–	–	–	p	02
Character-taxa of the Festuco-Sedetalia					
Tortella flavovirens (Bruch) Loesk.	a	m	–	–	–
Arenaria serpyllifolia	–	–	p	p	a
Ranunculus bulbosus	–	–	r°	r	p
Achillea millefolium	–	–	–	m	a
Vicia sativa ssp. *augustifolia*	–	–	–	r	p
Geranium pusillum	–	–	–	p	p
Trifolium striatum	–	–	–	p	r
Galium verum	–	–	–	p	p
Veronica arvensis	–	–	–	p	a
Medicago arabica	–	–	–	p	a
Character-taxa of the Arrhenatherion elatioris					
Bellis perennis	r	–	r	p	a
Cerastium holosteoides ssp. *triviale*	–	–	r°	m	m
Plantago lanceolata	–	–	–	a	a
Trifolium dubium	–	–	–	p	a
Daucus carota	–	–	–	r	p
Other taxa					
Blue-green algae (Cyanophyceae)	07	08	01	–	–
Elytrigia pungens	02	02	m	p	r
Leontodon nudicaulis	r	–	p	a	m
Bromus mollis	p	–	m	m	m
Anagallis arvensis	r°	r°	r°	–	r
Brachythecium albicans B. & S.	p	–	p	p	a
Eurhynchium praelongum (Hedw.) Hobk.	p	–	p	r	–

Additional taxa: Rel. no. 1: *Polygonum aviculare* r°, *Bryum* sp. p, *Brachythecium compactum* Aust. p, *Tortella inclinata* (Hedw. f.) Limpr. p; Rel. no. 2: *Polygonum aviculare* r°, *Sagina maritima* a, *Spergularia marina* r°, *Cochlearia danica* r, *Amblystegium* cf. *juratzkanum* Schp. a, *Bryum* sp. r; Rel. no. 3: *Plantago major* r°, *Bupleurum tenuissimum* r, *Amblystegium serpens* B. & S. p; Rel. no. 4: *Vicia lathyroides* p, *Trifolium campestre* r, *Agrostis tenuis* 01, *Dactylis glomerata* r, *Cirsium vulgare* r; Rel. no. 5: *Festuca arundinacea* r, *Eryngium campestre* a, *Medicago lupulina* a, *Lepidium campestre* m, *Cirsium vulgare* r, *Potentilla reptans* r, *Ranunculus repens* p, *Trifolium pratense* r, *Senecio erucifolius* r, *Polygonum persicaria* p, *Centaurea pratensis* r, *Glechoma hederacea* r, *Cynosurus cristatus* r, *Brachythecium compactum* Aust. r.

Sagina maritima	*Cochlearia danica*
Parapholis strigosa	*Sagina nodosa*
Plantago coronopus	*Bupleurum tenuissimum*
Pottia heimii	

Locally also *Cynodon dactylon* is found (Table 6). This species, together with *Bupleurum tenuissimum*, is favoured by dike slopes facing south. Locally large populations of *B. tenuissimum* and *Sherardia arvensis* can develop on southern inner slopes of the sea-dikes, especially where the vegetation cover is open as a result of grazing or blighting by insolation. *Odontites verna* ssp. *serotina*, on the other hand, is nearly exclusively found on northern slopes. Communities of the Puccinellietum distantis (alliance Puccinellio-

Table 7. *Communities between the quay pavement of the tidal harbours of Waarde (W) (Zuid-Beveland) and near Zonnemaire (Z) (Schouwen); June 1965; for explanation of the cover–abundance symbols see Table 2, p. 430*

Number of relevé	1	2	3	4	5	6	7	8
Locality	W	W	W	W	W	Z	Z	Z
Area (m²)	0·6×3	3×10	2·5×5	2×6	2×4	2×5	2×4	1·2×5
Cover of phanerogams (%)	40	25	25	25	15	30	15	15
Character-taxa of the Puccinellio-Spergularion salinae								
Puccinellia fasciculata	03	–	–	–	–	–	–	–
P. distans	p	02	r	p	–	m°	p°	r
Spergularia marina	m	r	r	p°	–	–	p°	a°
Character-taxa of the Saginion maritimae								
Plantago coronopus	–	–	m	m	a	01	01	p
Sagina maritima	–	–	–	–	–	01	m	p
Character-taxa of the Polygono-Coronopion								
Poa annua	–	–	p	m	02	–	–	m
Sagina procumbens	–	–	–	01	m	–	r°	r°
Polygonum aviculare	–	–	–	m°	r°	–	–	a°
Coronopus squamatus	–	–	–	–	–	–	–	r
Matricaria matricarioides	–	p	–	p°	r°	–	–	p°
Character-taxa of the Glauco-Puccinellietalia								
Aster tripolium	r	a	–	–	–	r°	–	–
Glaux maritima	–	–	02	m	–	a°	a	a
Plantago maritima	–	r	p	r	–	–	–	–
Juncus gerardii	–	–	–	–	–	01	a	p
Festuca rubra f. *litoralis*	–	p	r	–	–	p°	–	–
Character-taxa of the Plantaginetalia majoris								
Plantago major	–	a	r	a	a	a°	m°	m°
Lolium perenne	–	r	–	p	p	a	–	p
Elytrigia repens	–	–	–	a	r	p°	p	–
Taraxacum sp.	–	–	–	r	r	–	–	r
Agrostis stolonifera	–	–	r	r	r	–	–	r
Potentilla anserina	–	–	–	a	r	a	–	–
Other taxa								
Atriplex hastata	r°	a	–	–	–	–	–	–
Elytrigia pungens	a	a	a	r	–	p°	–	–
Matricaria recutita	–	–	–	–	–	–	p°	01

Additional taxa: Rel. no. 1: *Suaeda maritima* r°, *Spergularia media* p; Rel. no. 2: *Puccinellia maritima* r; Rel. no. 3: *Festuca arundinacea* r; Rel. no. 4: *Dactylis glomerata* p, *Poa pratensis* r, *Trifolium repens* p; Rel. no. 6: *Puccinellia maritima* a, *Parapholis strigosa* r, *Bromus mollis* r°, *Pottia heimii* (Hedw.) Fuernr. p, *Tortula muralis* p; Rel. no. 8: *Stellaria media* r, *Trifolium repens* r, *Juncus bufonius* var. *ambiguus* (Guss.) Sch. & Thell. m.

Spergularion salinae) as well as those of the Saginion maritimae are also found between the quay pavement of tidal harbours, often accompanied by common roadside plants characteristic of communities of the alliances Polygono-Coronopion and Agropyro-Rumicion crispi (order Plantaginetalia majoris). Table 7 gives an impression of the floristic composition and structure of this type of vegetation.

Deposition of flotsam and treading both mark the tension- or stress-line between tidal and non-tidal habitats. Its characteristic species are few, but usually abundant, particularly those growing on the flotsam belts.

Dike faces splashed by sea-water during storms with a slight supply of tidal drift often show dominance of *Elytrigia pungens* over a broad range of the slopes. Burning of flotsam washed ashore in winter has a similar effect, but may locally also cause mass germination of *Bupleurum tenuissimum*. A few months after the burning of the flotsam and the vegetation (mostly carried out during freezing spring weather), vigorous seedlings of this species emerge, covering up to half of the black burned soil. In the course of the following years the numbers of individuals of this annual decrease gradually, simultaneously with an increased growth of the recovering *Elytrigia* turf. Probably the seeds of *Bupleurum tenuissimum* are able to maintain their viability for several years, until germination is stimulated, either by burning or, in a more natural way, by insolation. That this species is favoured by sparsely overgrown south-facing dike slopes, as well as the fact that the bulk of the seeds germinate in July and August before seed-ripening, supports this supposition. Obviously, similar phenomena hold for other Umbellifers such as *Daucus carota*, *Pastinaca sativa* and *Heracleum sphondylium*, as Roeleveld (1965) found that burning of sea-dike vegetation also induces mass germination of these species.

If little flotsam is washed against the dikes the salt-marsh vegetation changes more gradually into other communities. These communities differ strongly in floristic composition and structure as a result of human exploitation. Grazing promotes the development of Agropyro-Rumicion crispi communities with:

Festuca rubra f. *litoralis* Hack.	*Leontodon autumnalis*
Agrostis stolonifera	*Lotus tenuis*
Trifolium fragiferum	*Carex distans*
T. repens	

proposed by Westhoff, van Leeuwen & Adriani (1962) as a special suballiance (Loto-Trifolion). Frequently, these communities are intermingled with more common meadow species such as:

Lolium perenne	*Plantago major*
Poa pratensis	*Ranunculus repens*
Hordeum secalinum	*Bellis perennis*
Dactylis glomerata	*Cerastium holosteoides*
Cynosurus cristatus	

which may even dominate (Lolio-Cynosuretum and Poo-Lolietum). Locally *Eryngium campestre* and *Ononis spinosa* may be present. *Ononis* together with *Lotus tenuis* and *Agrostis stolonifera*, growing on the inner dike slopes, indicated after many years the dike-bursts of the flood disaster of 1 February 1953 (Roeleveld 1965). Little grazing or no human interference at all often leads to dominance of *Festuca arundinacea* (Potentillo-Festucetum arundinaceae). Mowing promotes dominance of *Dactylis glomerata*, *Elytrigia repens*, *Arrhenatherum elatius*, etc. (partly Arrhenatheretum elatioris).

Most dikes are thrown up with clay, but old sandy dikes exist in the neighbourhood of the coastal dunes, as well as dikes covered with wind-blown sand. Dependent on the mobility and thickness of the sand layer the latter bear a vegetation similar to that of dunes or dry grasslands. If much sand is deposited species are found such as:

Cakile maritima	*Sonchus arvensis*
Atriplex spp.	var. *typicus* Beck
Elymus arenarius	*Solanum dulcamara*
Elytrigia pungens	*Calystegia sepium*
	Convolvulus arvensis

If not grazed more stabilized sandy dikes are overgrown with Prunetalia (Berberidion) communities predominantly consisting of:

Hippophaë rhamnoides	*Rosa canina*
Crataegus monogyna	*R. rubiginosa*
Ligustrum vulgare	*Asparagus officinalis*
Sambucus nigra	*Solanum dulcamara*
Rubus spp. (especially	*Bryonia dioica*
R. ulmifolius)	*Lonicera periclymenum*

Grazed by cattle such old dikes may bear Festuco-Sedetalia communities, characteristic of the dry sandy soils of the inner dunes, which soils are usually poor in carbonates. From these communities the following species are represented on the sandy dike faces:

Festuca rubra	*Vicia lathyroides*
subvar. *arenaria* Hack.	*Leontodon nudicaulis*
Carex arenaria	*Taraxacum* spp., such as
Phleum arenarium	*T. tortilobum* Fl.
Sedum acre	*T. rubicundum* Dt.
Cerastium semidecandrum	*T. lacistophyllum* Dt.
Galium verum	*Trifolium dubium*
var. *maritimus*	*T. campestre*
Ranunculus bulbosus	*T. striatum*
Erodium cicutarium	*T. scabrum*

If these habitats contact other types of grassland, viz. those which are classified in the alliances Arrhenatherion and Agropyro-Rumicion crispi, species characteristic of other habitats sometimes intrude. For the *Trifolium* species Westhoff (1965) pointed out that in the stable transition zone to the Arrhenatherion especially *T. subterraneum*, *T. ornithopodioides* and *T. micranthum* find their niches, while *T. fragiferum*, *T. hybridum* and *T. repens* are more or less confined to the Agropyro-Rumicion crispi. The coastal parts of the island of Walcheren, with a pronounced Atlantic but relatively dry climate, appeared to be especially rich in *Trifolium* species (Westhoff 1965).

From the outer face of the sea-dike via the inner slope to those of the 'retired' embankments, gradient situations of decreasing marine influence and of increasing age and stability can be recognized. Owing to the irregular tracks of the dikes, these gradients are crossed by the position of the slopes as regards insolation and prevailing wind (air-borne salt), and by divergent human exploitation (Tables 8 and 9). Without entering far into these very complicated interrelations it can be stated that:

Table 8. *Two types of abandoned grassland communities on dike slopes in the isle of Zuid-Beveland; the first, arranged according to the occurrence of* Dianthus armeria, *developing on sandy clay soils, the second on heavier clay soils (from Sykora-Hendriks & Sykora* 1973)

Number of relevé	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Area (m^2)	25	8	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25	16
Date (1972)	7 July	11 July	17 Aug.	17 Aug.	6 July	19 July	6 July	6 July	1 Sept.	11 July	19 July	17 Aug.	25 Aug.	25 Aug.	7 Aug.	20 May	18 May	7 Aug.
Burning (x)	x		x		x		x	x	x			x		x	x	x		x
Aspect	S	SSE	SW	S	SE	S	SW	SSW	SSW	SSE	S	SW	SSE	ENE	SW	NE	NW	SE
Character-taxa of the Molinio-Arrhenatheretea																		
Plantago lanceolata	–	+	+	2	–	2	+	–	–	–	+	–	1	+	–	–	–	–
Centaurea pratensis	+	–	+	–	–	–	–	–	–	+	+	1	2	+	+	–	+	2
Rumex acetosa	1	+	–	–	2	+	–	1	+	–	–	–	+	–	+	+	+	–
Holcus lanatus	+	+	+	–	–	–	+	1	+	–	–	–	+	–	–	–	+	2
Cerastium holosteoides ssp. *triviale*	–	+	1	+	1	+	–	+	–	–	+	–	+	–	–	–	–	–
Vicia cracca	2	–	–	–	–	+	–	–	–	–	+–1	–	–	–	1	–	–	–
Dactylis glomerata	+	–	+	+	–	–	+	+	–	+	+	+	–	–	+	+	+	+
Lathyrus pratensis	–	–	–	–	–	+	–	–	–	–	+	–	+–1	+	–	+	2	–
Trifolium pratense	–	–	–	+–1	–	–	1	–	–	–	–	–	+	+–1	–	–	–	–
Ranunculus acris	–	–	–	–	–	–	+	+–1	–	–	–	–	+–1	–	–	–	+	–
Character-taxa of the Arrhenatheretum elatioris																		
Daucus carota	–	+	2	2	–	+–1	–	2	+–1	+–1	+	+	+	1	–	–	–	1
Arrhenatherum elatius	–	–	–	–	–	–	2	+	2	–	–	3	–	+	–	–	–	–
Trisetum flavescens	–	2	2	–	2	–	–	2	2	2	–	+	–	–	–	–	–	–
Anthriscus sylvestris	–	–	–	–	–	+	–	–	–	–	–	–	–	+	+	+	4	–
Pastinaca sativa	–	–	–	–	–	–	–	–	–	–	–	–	2	2	–	2	–	2
Character-taxa of the Agropyro-Rumicion crispi																		
Elytrigia repens	3	3	4	3	–	3	2	+	+	4	3	3	2	2	2	3	3	3
Agrostis stolonifera	–	–	+	–	–	–	–	–	+	–	–	–	–	–	+	–	–	+
Pulicaria dysenterica	+–1	–	–	+–1	–	–	–	–	–	–	–	3	–	–	–	–	–	–
Festuca arundinacea	–	–	–	+	–	–	–	+	+	–	–	+	2	4	1	2	2	–
Character-taxa of the Trifolio-Geranietea																		
Agrimonia eupatoria	–	1	+	+	2	2	1–2	+	–	2	1	1	+	+	2	–	+	–
Origanum vulgare	1	–	+	+	–	+	2	–	–	1	2	2	2	3	+–1	–	–	–
Dianthus armeria	2	2	2	2	1	1	1	1	+	+	+	+	–	–	–	–	–	–

Table 8 (*contd*)

Number of relevé	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Taxa characteristic of dry grasslands*																		
Senecio erucifolius	+	–	–	2	+	+	1	1	+	–	1	–	+	1	+–1	+	–	–
Achillea millefolium	1	1	2	–	1	+	–	+	+–1	1	–	–	+–1	+	–	–	+	–
Medicago lupulina	–	+–1	1	+	–	–	2	+	+	+	+	–	+	+–1	–	–	–	–
Poa pratensis	–	–	–	–	+	+	2	–	+	–	+	–	–	–	–	–	–	–
Crepis capillaris	–	–	1	–	+	+	–	+	–	1	+	–	+	–	–	–	–	–
Senecio jacobaea	–	–	+	–	–	+	–	–	–	+	–	–	+	–	–	+	–	–
Ononis spinosa	–	+	–	–	–	–	–	–	–	2	–	+	–	–	+	–	–	–
Hypericum perforatum	2	–	–	–	–	+–1	–	–	–	–	+	+	–	–	3	–	–	–
Lotus corniculatus	–	1	+	–	+	–	–	+	–	2	–	1	–	–	–	–	–	–
Hieracium pilosella	–	1	–	–	+	–	+	2	+	–	–	+	–	–	–	–	–	–
Character-taxa of the Rhamno-Prunetea																		
Rubus caesius	2	–	+	+	+	+	2	3	2	–	2	+–1	3	+	3	1	+	1
Crataegus monogyna	+	–	+	+	+	+	–	+	+	2	+	+	+	–	+	–	+	–
Ulmus glabra	–	–	+	–	–	–	–	–	–	–	+	+	–	–	+	–	–	–
Other taxa																		
Festuca rubra	2	–	3	–	5	–	+	+	3	–	+	3	3	2	–	+	2	2
Equisetum arvensis	+	2–3	–	2	–	+–1	2	+	+–1	1	1	+	+	–	1	–	–	2
Allium vineale	–	–	–	–	–	+	+	–	–	+	1	+	+	–	–	–	–	+
Vicia sativa	–	–	+	+	+	–	–	2	–	–	–	–	+	+	–	+–1	–	1
V. tetrasperma	–	–	–	–	–	+	+	–	–	–	–	+	+	–	+	–	–	–
Carex spicata	–	–	+	–	–	–	–	1	+	1	–	–	–	–	–	–	–	–
Glechoma hederacea	–	–	–	–	–	+	–	–	–	–	–	+	–	–	–	+–1	+	–
Lamium album	–	–	–	–	–	–	+	+	–	–	–	–	–	–	–	–	–	+
Convolvulus arvensis	–	+	+	–	–	–	–	–	–	–	–	–	+	–	+	–	–	1
Verbena officinalis	–	+	–	+–1	–	1	–	–	–	1	–	–	–	–	–	–	–	–
Cirsium arvense	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	2	+–1	+

Additional taxa: Rel. no. 1: *Agrostis tenuis* +, *Anagallis arvensis* +–1, *Phragmites australis* +–1, *Rubus ulmifolius* 2; Rel. no. 2: *Bromus mollis* +; Rel. no. 3: *Geranium molle* +, *Taraxacum* sp. +; Rel. no. 4: *Carduus crispus* +, *Galium aparine* +, *Lathyrus nissolia* +, *Potentilla anserina* +–1; Rel. no. 5: *Campanula latifolia* +, *Carduus crispus* +–1, *Carlina vulgaris* +–1, *Geranium molle* 1, *Inula conyza* 2, *Prunus spinosa* 2; Rel. no. 6: *Agrostis tenuis* +; Rel. no. 7: *Calystegia sepium* +, *Cynosurus cristatus* +, *Agrostis tenuis* +, *Lysimachia nummularia* +, *Trifolium repens* +; Rel. no. 8: *Phragmites australis* 1, *Rumex conglomeratus* +, *Stellaria media* +, *Valeriana officinalis* +; Rel. no. 9: *Lolium perenne* +; Rel. no. 11: *Eupatorium cannabinum* +, *Matricaria recutita* +, *Prunus spinosa* +; Rel. no. 12: *Geranium molle* +, *Inula conyza* +–1, *Trifolium dubium* +; Rel. no. 13: *Rosa canina* +, *Tragopogon pratensis* +, *Trifolium dubium* +; Rel. no. 14: *Potentilla reptans* +–1, *Tragopon pratensis* +; Rel. no. 15: *Lysimachia nummularia* +–1, *Rhinanthus minor* +; Rel. no. 16: *Poa trivialis* +, *Rumex crispus* +, *Taraxacum* sp. +, *Urtica dioica* +; Rel. no. 17: *Poa trivialis* +, *Ranunculus repens* +; Rel. no. 18: *Calystegia sepium* +, *Phleum pratense* +, *Ranunculus repens* 1.

Estimation of cover–abundance according to Braun-Blanquet (1928): r = 1–3 individuals; + = few individuals; 1 = individuals rather numerous, cover less than 5%; 2 = individuals very numerous, cover less than 5%, or 5–25% cover; 3 = 25–50% cover; 4 = 50–75% cover; 5 = 75–100% cover.

* Mainly classified into the classes Festuco-Brometea and Festuco-Sedetalia.

Table 9. *Two types of shrub communities (differential taxa* Geum urbanum *and* Prunus spinosa) *on dike slopes in the isle of Zuid-Beveland (from Sykora-Hendriks & Sykora* 1973); *for explanation of the cover–abundance symbols see Table* 8, *p.* 451

Number of relevé	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Area (m²)	16	25	25	100	25	25	25	16	25	25	25	25	16	25	25	25
Date (1972)	23 June	8 Aug.	27 July	2 Aug.	27 July	28 June	7 July	1 Aug.	25 Aug.	27 Aug.	18 July	7 Aug.	25 Aug.	8 Aug.	27 Aug.	29 June
Aspect	WSW	SE	E	SSW	E	NE	SE	NNW	SW	N	W	SW	SW	SE	NNE	SW
Character-taxa of the Berberidion																
Crataegus monogyna	3	2	5	4	4	+	2	3	3	4	2	5	3	+	3	2
Rubus caesius	2	3	–	+	2	3	3	+	3	+	2	+	1	2	+	2
Rosa canina	2	+	–	–	–	2	2	–	3	2	–	–	–	–	–	3
Rubus ulmifolius	+	–	3	2	–	–	–	–	–	–	–	–	–	–	–	–
Humulus lupulus	–	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–
Ligustrum vulgare	–	–	–	–	–	–	–	–	2	4	–	–	–	–	–	–
Prunus spinosa	–	–	–	–	–	–	–	–	–	–	3	+	+	3	2	3
Character-taxa of the Alno-Padion																
Ulmus glabra	–	3	–	+	4	5	4	4	3	–	2	2	5	4	5	2
Viola odorata	–	–	2	+	+	–	–	–	–	–	–	2	+	2	+	+–1
Fraxinus excelsior	–	4	–	2	2	–	3	–	–	–	–	–	–	–	3	–
Character-taxa of the Artemisietalia vulgaris																
Galium aparine	2	+	+	+	+	3	2	–	4	–	+	+	2	2	+	+
Urtica dioica	2	+–1	1	1	+–1	1	2	1	–	–	–	+	–	+	–	+
Glechoma hederacea	+–1	–	+	4	–	3	2	+	–	–	–	3	2	3	–	–
Geranium robertianum	–	–	–	+	–	–	–	2		–	–	2	3	+	–	–
Aegopodium podagraria	–	–	+–1	–	3	–	–	–	–	–	–	–	–	–	–	1
Geum urbanum	+	+–1	+–1	2	+	–	–	+–1	–	–	–	–	–	–	–	–
Character-taxa of the Agropyro-Rumicion crispi																
Poa trivialis	–	+	+	3	2	–	2	+	–	–	–	2	–	+	–	–
Elytrigia repens	+	+	–	–	–	2	–	–	–	+	–	–	+	–	–	–
Lysimachia nummularia	–	2	–	+	–	–	–	–	–	–	+	–	–	–	–	–
Other taxa																
Anthriscus sylvestris	2	2	+–1	–	–	2	+	+	–	–	+	–	–	+	3	+
Equisetum arvense	+	–	+	–	–	–	–	–	–	–	1	–	+–1	+	–	–
Agrimonia eupatoria	–	–	–	–	–	+	–	–	–	–	+–1	–	+	–	–	–
Dactylis glomerata	+	+	+	–	+	2	–	2	–	+	–	+	+	–	–	–
Festuca rubra	–	–	2	–	–	–	–	–	2	–	2	–	+	–	–	–

Additional taxa: Rel. no. 1: *Agrostis stolonifera* +, *Alliaria petiolaris* +, *Calystegia sepium* +, *Hedera helix* 2, *Lamium album* 1, *Taraxacum* sp. +; Rel. no. 2: *Fragaria vesca* 1; Rel. no. 3: *Holcus lanatus* +, *Populus alba* +, *Rumex acetosa* +; Rel. no. 4: *Bryonia dioica* +, *Taraxacum* sp. +, *Torilis japonica* +; Rel. no. 5: *Chelidonium majus* +, *Crepis capillaris* +, *Daucus carota* +, *Lapsana communis* +, *Stellaria media* +; Rel. no. 6: *Arrhenatherum elatius* 3, *Convolvulus arvensis* +, *Eupatorium cannabinum* +, *Lysimachia vulgaris* 1, *Poa pratensis* +, *Ranunculus acris* +, *Rumex acetosa* +, *Valeriana officinalis* +; Rel. no. 9: *Calystegia sepium* +; Rel. no. 11: *Centaurea pratensis* 1, *Eupatorium cannabinum* 2, *Festuca arundinacea* +, *Lathyrus pratensis* +, *Origanum vulgare* 2, *Rhinanthus minor* +, *Valeriana officinalis* 1; Rel. no. 12: *Convolvulus arvensis* +–1, *Sonchus asper* +; Rel. no. 13: *Convolvulus arvensis* +, *Rosa dumetorum* 2, *Torilis japonica* +; Rel. no. 15: *Chelidonium majus* 2, *Lamium album* 2; Rel. no. 16: *Agrostis stolonifera* +, *Stellaria media* +–1.

(1) where human influence is slight or absent a mosaic can develop, consisting of shrubs (alliance Berberidion, order Prunetalia) and tall herbs (characteristic of the alliance Trifolion medii, order Origanetalia vulgaris, class Trifolio-Geranietea sanguinei, and of the alliance Arction, order Artemisietalia vulgaris);
(2) mowing promotes the extension of the tall herbs and the establishment of representatives of the Arrhenatheretum elatioris (order Arrhenatheretalia);
(3) grazing favours the development of Lolio-Cynosuretum communities, often—particularly at the foot of the dikes—joined by Agropyro-Rumicion crispi elements;
(4) burning appears to promote mass development of geophytes and hemicryptophytes (e.g. *Elytrigia pungens*, *E. repens*, *Dactylis glomerata*, *Festuca arundinacea*) and of Umbellifers such as *Heracleum sphondylium*, *Daucus carota*, *Pastinaca sativa* and *Bupleurum tenuissimum*;
(5) planting with trees, especially poplars, reduces the vegetation to a minority of species, and will induce settlement of Artemisietea-species, such as *Urtica dioica*, *Cirsium arvense*, owing to the shading and manuring influence of the leaves;
(6) heavy fertilizing has a similar effect to (5);
(7) a closed, impermeable cover on the surface of the road (asphalt) on the crown of the dike leads to a reduction of the number of species on the slopes, owing to an increase of instability at the slopes, as surface water running down from the pavement affects the hydrology of the soil. It was found that there was a relation between the construction of an asphalt pavement and the total disappearance of *Cirsium eriophorum* on the slopes of a dike in the island of Zuid-Beveland. In the south-west part of the Netherlands this species is confined to these dike slopes from of old, and grows there in a narrow contact zone between Agropyro-Rumicion communities (Potentillo-Festucetum arundinaceae) along the road, and the Arrhenatheretum underneath (Westhoff & den Held 1969).

The river dunes and dike faces as habitats for plant migration

Another ecologically interesting group of species occurs on 'river-dunes'. These are sandy, dry and sun-warmed elevations on the inner banks of the meanders deposited by the river-water. These elevations may be relatively poor to rich in nutrients owing to flooding and grazing intensity, but are always more or less influenced by the calcareous river-water via the groundwater. Many of the plant species characteristic of these habitats have a subatlantic or continental area of distribution, running downwards in a northern and western direction into warm, sandy and calcareous habitats within the river valleys by 'steps and jumps'. These communities have been classified as associations of the alliances Mesobromion (Brometalia) and Sedo-Cerastion (Festuco-Sedetalia), and show a floristic affinity to the communities of the dry grasslands of the inner coastal dunes (Westhoff 1966; Neijenhuijs 1968). According to Cohen-Stuart & Westhoff (1963) the most extensive habitats and best developed—although not the richest—communities are not found in the east of the Netherlands, but in the west, in the area which den Hartog (1961) named the 'stuw-zone'. This zone forms the innermost part of the freshwater tidal area adjacent to the fluvial region proper, and is characterized by vertical tidal movements combined with a constantly seaward-directed river current. The periodic tidal fluctuations will contribute more spatial differentiation to this riparian habitat than the episodic ones inherent in the fluvial region proper, notably as regards carbonates and soil moisture. Further downstream, in the freshwater tidal zone (Biesbosch) and in the brackish zone the fluvial elevations ('river dunes') largely lose their gradient character as a result of larger tidal differences, deposition of silt, and predominating salinity (see also Cohen-Stuart & Westhoff 1963). Before embankment was practised, during transgression periods when the sea broke into the coastal area, sufficient sand was supplied to form highly accreted estuarine sand deposits. During periods of ingression of the sea, these deposits may then have obtained a gradient character comparable to that of the 'river-dunes'. Therefore, it is assumed that the plant species characteristic of these habitats may have colonized the estuarine region from two sides, both from the river valleys and from the coastal dunes. Most of these species are thermophilous. Consequently they are mainly found on slopes facing south. Representatives growing on southern dike faces are those faithful to the Mediterranean–Atlantic ruderal association Medicagini-Toriletum nodosae Westhoff 1969 (Alliance Helminthion echioidis). The most important species, which probably penetrated into the estuarine region from the south-west are *Medicago arabica, Torilis nodosa, Picris echioides, Lactuca saligna, Petroselinum segetum, Carduus tenuiflorus*, and perhaps *Centaurea calcitrapa*. Other species which may have penetrated from the coastal dunes into the estuaries and the river valleys are *Phleum arenarium, Cynoglossum vulgare, Orobanche purpurea, Trifolium subterraneum*, and *Poa bulbosa*.

Penetration via the dike faces from the river valleys into the coast, however, must have been much more common, as many river valley species terminate their area of distribution in the Dutch estuarine region or in the adjacent coastal dunes. These species can be divided into different ecological groups, mainly coinciding floristically with distinct vegetation units.

On mostly sandy, but always dry to very dry calcareous soils, in sun-warmed places, species characteristic of the classes Festuco-Sedetalia and Festuco-Brometalia are found:

Ranunculus bulbosus	*Sedum acre*
Eryngium campestre	*Vicia lathyroides*
Trifolium campestre	*Medicago minima*
T. striatum	*Carlina vulgaris*
Taraxacum tortilobum Fl.	*Artemisia campestre*, etc.
Cerastium arvense	

On generally more clayey and thus less dry soils under stable environmental circumstances, such as some old dike faces, tall herbs characteristic of the class Trifolio-Geranietea sanguinei develop: *Origanum vulgare, Agrimonia eupatoria, Senecio erucifolius, Galium mollugo, Lathyrus nissolia*, etc.

Under still more humid but particularly eutrophic and therefore less stable conditions, species faithful to the order Arrhenatheretalia are found, dependent on the nature of human exploitation of the dikes, for instance:

Dactylis glomerata	*Pastinaca sativa*
Alopecurus pratensis	*Heracleum sphondylium*
Festuca pratensis	*Trifolium dubium*
Lathyrus pratensis	*Symphytum officinale*
Ranunculus acris	*Rumex obtusifolius*
Chrysanthemum leucanthemum	*Carduus crispus*
Daucus carota	*Verbena officinalis*

Together with others the last mentioned four species indicate the connection with the still more anthropogenic communities classified into the Artemisietea vulgaris. Along the foot of the dike, instability increases owing to increased seepage processes, and a variety of Agropyro-Rumicion crispi species, dependent on salinity fluctuations and human exploitation, comes to the fore.

CONCLUSIONS

Human impact in the estuarine water–land boundary leads to both convergence and divergence in environmental conditions. From this ecological point of view the side-effects of embanking coastal areas can be subdivided into negative and positive ones. Negative ecological side-effects decrease ecological variety-in-space and enlarge contrasts-in-time, converging ecological extremes both in space and in time. Positive side-effects induce an increase of ecological variety-in-space and diminish contrasts-in-time, diverging ecological extremes.

Embanking *per se* promotes convergence of salt- and freshwater conditions, and also changes the environmental conditions on either side of the dikes. In both types of side-effects, it appears that the negative, converging ones and their impact predominate outside the sea-dike, while the positive side-effects do so in the polderland.

Several examples support the view that former embankments must have stimulated the establishment of many species of phanerogams and their associations in the poldered areas of the south-west Netherlands, the dikes themselves representing special habitats as pathways for immigration.

However, former embankments must have decreased drastically the ecological variation of the tidal areas, especially the variation developing above the spring-flood zone and in the transition zone to the dunes. In this way various types of habitat, characterized by a low salinity and fluctuating soil moisture, became rare or disappeared completely. Special features of such habitats are a low degree of eutrophication, a high degree of humification and divergent contents of lime: their genesis depends on predominance of climatic influences over tidal ones. Consequently, the prevalent remaining habitats of present times are mainly characterized by vigorous mineralization and a fair content of lime and nutrients (eutrophic) owing to preponderating tidal influences.

In addition to these negative side-effects, embanking generally leads to an overall preponderance of erosion over sedimentation processes, especially at the level where the mud flats change over into the real salt marsh (Mean High-Water line). Steep erosion edges very often develop. *Spartina townsendii* s.l., a plant with a remarkable capacity to fix silt, seemed to man to be a solution to the problem of defending this foreshore. Ecologically, however, this taxon introduced a new disturbing element in the tidal-marsh ecosystem.

The close association of man's former reclaiming activities with natural topographic elements in the boundary system between water and land resulted ultimately in the establishment of more diverging than converging conditions. In the course of time, however, man's technical prowess enabled him to deviate more and more from natural topography and to enclose ever vaster expanses in his embankments. Besides this spatial aspect, developing reclamation techniques enabled man to interfere more and more with ecological conditions, transforming them more drastically and more frequently. In this manner an ever-increasing similarity and uniformity is introduced in the course of time reflected by the structure and vegetation of the successively poldered landscapes.

At present this technical progress is so far advanced that coastal reclamation and defence engineering is more a question of economics than of technology. Therefore, in the Netherlands the Central Bureau voor de Statistiek (Central Statistical Office) has started an approach to evaluate natural and semi-natural resources in terms of economics against the economic value of civil-technical and industrial works, including those initiated for recreational purposes. In this evaluation the aim is particularly to elucidate in how far the business and socio-economic advantages of those works, after deduction of their negative social and ecological side-effects, offset the business and socio-economic advantages involved in the preservation of the present environment. It is emphasized that the hitherto neglected analysis of the economic disadvantages of present and projected technical activities should be thoroughly examined.

Within our scope such an evaluation will be of some importance, as the coastal margin, including its estuarine identations, is one of the elements of the biosphere most intensively occupied by man. Therefore, the report of the Countryside Commission (1969) based on a study by the British Nature Conservancy and dealing with the question how the conflicting demands on the coastal area can be reconciled with the need to preserve the coast's natural features, may be a start in the scope of this approach.

However, all these attempts to save Nature based upon economic considerations are no ultimate solutions. If economic motives are exclusively considered, nature conservation is accepted only in so far as it favours human welfare. The reverse, erecting an ecological framework within which economical activities may go their own short-term way, seems to have more prospect of success. Fundamentally it depends on the ethics and philosophy of life of both the individual and mankind as to which principles are ultimately used in practical management of Nature.

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SUMMARY

Former embanking and draining activities are closely associated with natural geomorphological components and tidal processes inherent in the water–land boundary. These components, named 'selectors' by van Leeuwen (1967), appeared to help man in selecting his own environment. Also this close connection is shown in language and family names.

The ecological side-effects of embanking and drainage are both negative and positive. The negative side-effects are apparent mainly outside the sea-dike, and the positive ones in the polderland. The dike itself forms a special habitat as a pathway for immigration. Both types of side-effects are discussed in their connection with embankment and drainage works as well as in their ecological consequences for plant life (especially that of halophytes). The problems of river fluke disease and of the distribution of some other animal groups are briefly mentioned.

Finally it is stated that at present modern coastal reclamation and defence engineering is more a question of economics than of technology. A plea is made for an evaluation of the real economic advantage of such works against the social advantages of the present state of the coast's natural features.

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